A study on the biology of four Tasmanian cushion species

by

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Submitted in fulfilment of the
requirements for the degree of

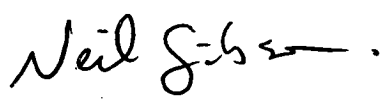
Doctor of Philosophy

UNIVERSITY OF TASMANIA
HOBART

December 1988

DECLARATION

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university and contains no copy or paraphrase of material previously published or written by another person, except where due reference is made in the text.



NEIL GIBSON

ABSTRACT

Donatia novae-zelandiae, Abrotanella forsteroides, Dracophyllum minimum and Phyllachne colensoi are four superficially similar bolster species found in the Tasmanian alpine vegetation. The ecological differentiation of the ranges of these species, the dynamics of the formation and persistence of complex mosaics of two or more of these species and the functional significance of the bolster form were areas in which there were many hypotheses but few data.

Growth studies undertaken in Tasmania showed significant seasonal differences in the competitive ranking of cushion species. Annual shoot production ranged from 426-709 g/m^2 for A. forsteroides; 359-477 g/m^2 for D. minimum; 322-572 g/m^2 for D. novae-zelandiae; and 282-285 g/m^2 for P. colensoi. These figures are greater than those reported from cushion communities in New Zealand and from physiognomically similar communities in the northern hemisphere, probably reflecting the maritime climate and the longer growing season of the Tasmanian alpine zone.

Seed production was highly variable between sites with D. novae-zelandiae producing between 2,370-38,900/m^2 and D. minimum between 0-17,140/m^2 over the 1982/83 summer. Estimates of the lateral growth rate of A. forsteroides in open situations on peat substrates ranged from 6.7-14.7 mm diameter increase/year. D. minimum seedlings on rocky and well drained mineral soils only achieved lateral growth rates of between 0-7 mm/year.

Data from the growth studies showed that cushion distribution at Mt. Field could not be explained by either soil moisture or soil nutrient preferences. Growth was found to be highly variable from year to year and season to season both between species and within species over their altitudinal ranges. It was concluded that interspecific competition between bolster species plays little role in determining their overall distribution patterns. Climatic modelling suggests that distribution of the species is primarily controlled by the temperature (this is presumed to relate to competition from taller growing shrubs and graminoids) and past climatic history. Donatia novae-zelandiae, Abrotanella forsteroides, and Dracophyllum minimum may still be expanding their ranges following the climatic amelioration since the height of the Last Glacial.

Investigations into the dynamics of a bolster heath modified and improved the model proposed by Jackson (1981). Pathways of succession due to changes in water table appear to result from complex interactions between the water table level, propagule source and species already present on the site. Data from a peat core indicate that once bolster communities have become established, they can persist for very long periods. In the succession from bare ground to closed bolster communities there is a general lack of pioneering species. Results from the growth study, the patterns of reinvasion of drained tarns and studies of permanent photopoints are consistent with the view that succession in bolster communities is best described by inhibition or tolerance models (Connell and Slatyer 1977). Competition appears to play an important role at the establishment phase in mature bolster communities but once establishment has occurred it is much less important. Competition also appears to be of little importance in the building phase of bolster communities in highly stressed environments.

Attempts to elucidate dynamics by studying pattern in mosaic bolster communities using spectral analysis failed due to the inability of this technique to separate patch size and inter-patch distance.

The roots of all cushion species freeze at temperatures between -1° and -5° C. Nonetheless the insulating properties of cushion peats are so effective that it is unlikely that root freezing ever occurs with adult plants in the field, at least under the present climatic conditions. Similarly the thermal characteristics of peat soils are such that seedling death due to root freezing would also be an extremely rare event.

Short interval temperature measurements showed A. forsteroides capable of achieving cushion surface temperatures 10° C above ambient temperatures. It is suggested that this feature of cushion plants may allow them to undertake photosynthesis under otherwise limiting conditions and may significantly extend their growing season.

Anatomical investigation of the four cushion species showed a highly variable internal structure. This diversity is difficult to interpret. The scleromorphic nature of most of the species may be related to nutrition. The xeromorphic features exhibited by the four species and the thermal characteristics of the

cushion form are inconsistent with the hypothesis that these species suffer significant periods of water deficit.

ACKNOWLEDGEMENTS

I would like to thank Bill Jackson and Alison Turner who first kindled my interest in the ecology of alpine Tasmania in general and cushion plants in particular; and Jamie Kirkpatrick for his supervision during the following years. Many other people also assisted in a of variety ways, large and small, in the course of this work. To all of them I would like to record my thanks.

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CHAPTER 1 INTRODUCTION

Cushion plants are an unusual life form found world wide (Rauh 1939, Godley 1978) that reach their maximum expression in the alpine and subalpine regions of Tasmania, New Zealand, South America, the subantarctic islands and New Guinea (Rauh 1939, Taylor 1955, Godley 1978, Pisano 1983, Wardle 1985, Gibson and Hope 1986). They are chamaephytes or hemicryptophytes with closely packed shoots and very short internodes which form compact, often hard, cushions ranging in shape from almost flat to almost hemispherical. Individuals of some species can grow to more than three metres in diameter. Alternatively, several species may coalesce to form extensive mosaics (Heilborn 1925, Gibson and Kirkpatrick 1985a).

The cushion form can be produced by several different structural morphologies, making any precise definition of the term cushion plant difficult. Some species are facultative cushions, producing the form only in particular environments.

In a world-wide survey of cushion plants Rauh (1939) used the term for any species that was capable of producing a recognizable cushion. He subdivided cushion plants into five primary types on gross structural morphology (table 1-1), although not all categories are mutually exclusive even in the adult stage. The hard cushion species common in Tasmania and New Zealand fall into his categories of spherical and compact cushions (types 1c, 1d, 3 - table 1-1). The major problem with the Rauh definition is that the categories are overlapping. In this thesis cushion plants have been defined as :

Bolster (or hard) cushion plants - any species that growing singly takes on a hemispherical or subhemispherical shape due to the close branching of its shoots and very short internode lengths. The hardness of the resulting cushion is such that the surface can support the weight of a small mammal without deformation. Different bolster species can coalesce to form extensive flat mosaics. The term bolster includes types 1c and 3 of Rauh's classification (table 1-1). Donatia novae-zelandiae[1] is a typical example of this cushion type.

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1 Nomenclature follows Curtis (1963,1967), Curtis and Morris (1975), Costin et al. (1979), Mark and Adams (1979) and Taylor (1955) except where otherwise stated. Vegetation terminology follows Kirkpatrick (1983).

Table 1-1. Rauh's classification of cushion plant types, where cushion plant is defined as any species capable of assuming a cushion form (Rauh 1939).

1. TRUE CUSHION PLANTS

The cushion form in these species is genetically fixed and results from the systematical relationship of the even radial growth of numerous often closely packed shoots with little apical dominance, resulting in flat hemispherical surfaces. In compact species peat accumulation results. These species have a persistent tap root, though adventitious roots may also develop. They can be split into four subgroups.

a) Tree cushions
b) Spherical shrubs
c) Spherical cushions proper — non peat-accumulating; peat-accumulating
d) Flat cushions — non peat-accumulating; peat-accumulating

2. CREEPING CUSHIONS

Those species of mat cushion which form by lateral branches spreading in all directions and which root adventitiously from nodes. Persistent taproot present.

3. COMPACT CUSHIONS

Morphologically identical to true cushion plants. However a persistent taproot is replaced by adventitious rootlets.

4. ROSETTE CUSHIONS

Formed by the production from a young plant of lateral branches with a terminal rosette which in turn roots and produces further rosettes, generally with gradually decreasing internode length. The result is a dense solid cushion of somewhat interconnected rosettes.

5. CUSHION MOSSES

All moss species that product the cushion form.

Flat cushion plants - any species that growing singly takes on a flat and circular shape which does not result from a trailing prostrate branching pattern. This type of cushion plant conforms with type 1d of Rauh's classification (table 1-1) and is typified by Oreobolus pumilio.

Mat shrubs - are any species that growing singly can take on a circular shape which results from prostrate branches which may or may not be capable of rooting at the nodes. This group includes Rauh's types 2 and 4 and is typified by Pimelea pygmaea.

World-wide, cushion plants have been recorded from 34 families (Godley 1978). In Australasia, they are found in 27 families in alpine and subalpine areas of Tasmania, Australia, New Zealand, New Guinea and on subantarctic Macquarie, Auckland and Campbell Islands (Oliver and Sorensen 1951, Moar 1958, Gibson and Hope 1986). Within this Australasian region there is a strong relationship between the cushion floras at family and generic level, although each area has produced its own suite of species (Gibson and Hope 1986).

The environments in which these species occur are generally very rigorous, with low temperatures, short growing seasons, periods of snow lie, severe frost action, high winds, ice ablation, physical drought, physiological drought and low soil fertility being common. It has been suggested that one or other of these factors acting alone or in conjunction may have been the causal factor in the evolution of the cushion life form (Bliss 1956, 1971; Spomer 1964; Tiffney 1972; Billings 1974a; Hedberg and Hedberg 1979; Ruthsatz 1979). Given the large number of morphological types of cushion plant, the large number of families from which they have evolved, and the range of environments they occupy, it is highly unlikely that there is a single or even a few causal factors that have been critical in the evolution of this life form (Gibson and Hope 1986).

In the northern hemisphere the major environmental gradients determining vegetation patterns in alpine and tundra areas are altitude, exposure and period of snow lie, with cushion plants occurring as small individuals in fjaeldmarks on snow free summits and ridges (Bliss 1971, Billings 1974a). Cushion plants are most prominent in the subalpine and alpine regions of South America, New

Zealand, the subantarctic islands and Tasmania. In South America extensive areas of cushion vegetation are found with the Magellanic tundra complex described by Pisano (1983). Here community distribution appears to be controlled by altitude, precipitation and snow lie, similar to the major environmental gradients in the northern hemisphere. The most extensive cushion bogs in the world are probably found in southern South America extending from 45° S to 55° S (cf. Bliss 1971). Further north along the Andes large areas of cushion vegetation are also found in the arid puna region of north west Argentina (Ancibor 1980,1981).

In New Zealand cushion plants occur from sea level to high alpine zones mainly in habitats subject to some degree of stress (e.g. high water tables, long snowlie, high wind exposure, high temperatures). The distribution of South Island cushion communities surveyed by Gibson and Kirkpatrick (1985a) was found to be closely related to particular geomorphic environments. No overall phytosociological study of the New Zealand alpine vegetation has been undertaken but regional studies suggest that lithology, altitude and length of snow lie are the most important factors determining vegetation distribution (Mark and Bliss 1970; Burrows 1977a,b). In contrast to their distribution in the northern hemisphere, cushion plants in New Zealand occur in highly exposed, snow free areas as well as very late snow beds. In addition cushions also dominate some alpine and subalpine bogs, a situation from which they are completely absent in the northern hemisphere (Burrows 1977a,b).

On subantarctic Macquarie, Marion and Heard Islands the bolster species Azorella selago dominates in exposed areas subject to the constant westerly wind. In these environments seasonal snow lie plays little part in determining the vegetation patterns (Taylor 1955, Huntley 1971, Hughes 1987). On subantarctic Campbell and Auckland Islands cushion plants occur in extensive blanket peat bogs dominated by Oreobolus pectinatus and Phyllachne clavigera (a closely related if not conspecific species with Phyllachne colensoi) which occur down to sea level (Oliver and Sorensen 1951, Moar 1958, Dobson 1979). The factors controlling vegetation patterns on these islands have not been fully investigated.

In Tasmania there are four superficially almost identical bolster species, Abrotanella forsteroides (Hook f.) Benth. (Asteraceae), Dracophyllum minimum (Epacridaceae), Phyllachne colensoi (Stylidiaceae) and Donatia

novae-zelandiae (Donatiaceae). A. forsteroides and D. minimum are Tasmanian endemics while D. novae-zelandiae and P. colensoi also occur in New Zealand. Both these latter species have close relatives in South America.

These four bolster species have been suggested to form an overlapping replacement series along a south west to north east floristic gradient (Kirkpatrick 1982). This gradient is believed to reflect changes in soil fertility. Cushion species distribution patterns have also been correlated with altitude and soil drainage (Kirkpatrick 1983, Kirkpatrick et al. 1985). Little is also known of the processes of vegetation dynamics in bolster communities. Jackson (1973, 1981) has suggested that they form part of a simple cyclical succession with low coniferous heath driven by changes in the height of the water table. Kirkpatrick and Gibson (1984) have recently suggested that the dynamics of these vegetation types are considerably more complex. No long term successional studies have been carried out in bolster communities.

The occurrence of convergent evolution to particular lifeforms has been noted in geographically isolated harsh environments. It is generally believed that the particular lifeform buffers the organism from harsh environmental conditions (Mooney and Dunn 1970, Smith and Young 1987 and others). The functional significance of the cushion form has been little studied.

This thesis investigates three major interrelated aspects of cushion plant biology :

1. the ecological differentiation of the ranges of the four species.
2. the dynamics of the formation and persistence of complex mosaics of two or more cushion plant species.
3. the functional significance of the bolster form.

The work reported here has concentrated on the four green bolster species but aspect of the biology of another Tasmanian bolster species, Pterygopappus lawrencii, have been addressed in the sections dealing with cushion plant community dynamics. This sage coloured species forms a softer bolster than the four species described above.

The first section of this thesis deals with the ecological differentiation of the geographical ranges of A. forsteroides, D. novae-zelandiae, D. minimum and P. colensoi. These four species not only show a high degree of morphological

convergence but also a high degree of range overlap (figure 1-1, Brown et al. 1983a, Kirkpatrick et al. 1985). No experimental data are available to test Kirkpatrick's hypotheses that cushion plant distribution is controlled by soil fertility, altitude or drainage. To investigate these hypotheses detailed environmental and growth studies were carried out on the four Tasmanian cushion species at Mt. Field in central southern Tasmania, one of the few areas where all four species co-occur. The research hypotheses were -

1. there are interspecific differences in annual and seasonal above ground biomass production .

2. there are differences in above ground biomass production and reproductive success within and between species over an altitudinal gradient.

3. there are significant differences in annual and seasonal soil moisture conditions between sites dominated by the different species.

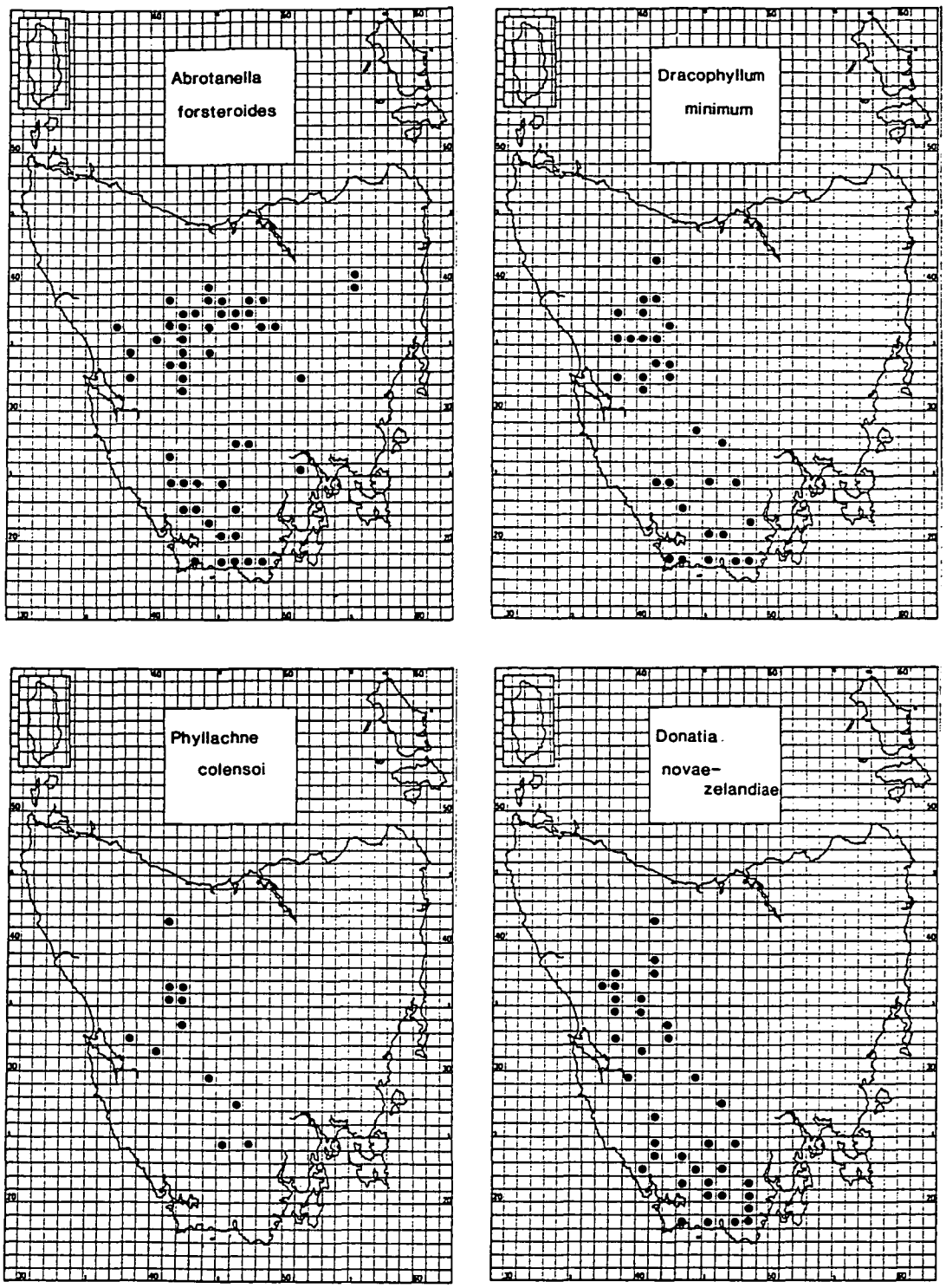
4. there are significant differences in the soil nutrient levels between sites dominated by the different species.

The results from these studies are reported in Chapters 2. Estimates of the rate and variability of lateral growth of bolsters were also obtained from a study of the reinvasion by bolsters of areas burnt by fires of known ages (chapter 3). Comparative growth data on bolsters from subantarctic Macquarie Island was collected during the course of this study and is reported in Appendix 3.

Data from the growth studies and those derived from climate modelling allowed the development of broad scale distributional models. The results of this exercise are presented in Chapter 4.

One of the most remarkable communities in which cushion plants occur in Tasmania are the mosaic cushion heaths (Gibbs 1920, Gibson and Kirkpatrick 1985a). These communities consist of complex intermixtures of several cushion species forming extensive flat or gently undulating surfaces of high species richness (commonly 30 species/m^2).These communities can be very extensive (several hectares in area) and are apparently stable through time. An

Figure 1-1 Distribution patterns of the four Tasmanian bolster species based on a 10 km grid. (After Brown et al. 1983, Gibson and Kirkpatrick 1985a, Kirkpatrick et al. 1985).



investigation of the mechanisms that allow the formation and persistence of these mosaics constitutes the second part of this thesis.

Initially two hypothesis were investigated

1. the succession from bare ground to mosaic cushion heath follows the classic facilitation model.

2. the mosaic cushion heaths are stable in the mid to long term (5-1000 years).

The first hypothesis was tested using data collected from a series of drained tarns of different ages covering the complete sequence from bare ground to mosaic cushion heath. The second hypothesis was investigated by cuticular analysis of a peat core 1 m in length collected from mosaic cushion heath damming a tarn. These results are reported in Chapter 5.

The results from these studies suggested that once a cushion species had become established it was highly likely to persist through time. This implied that recruitment into a mosaic would initially be multi-aged until full cover was achieved and thereafter little recruitment would occur. This hypothesis was investigated in two ways, initially pattern analysis of 2 m x 2 m quadrats was carried out using two-dimensional spectral analysis and concurrent model building. Later a series of five year old permanent photopoints were analysed covering a range of cushion communities from actively expanding cushions, through a stable mosaic community to a degenerate community. These change primarily resulting from changes in the water table. The results of these studies constitute Chapters 6 and 7.

The final section of this thesis deals with the functional significance of the cushion form. In Tasmania it has been suggested that the cushion form may minimize transpiration and damage from ice abrasion (Kirkpatrick 1983), have temperature moderating properties that prevent shoot death for brief periods at high or low temperatures (Turner 1981), or modify the local environment (Martin 1940, Jackson 1973).

Turner (1981) examined the functional significance of the cushion form in relation to subzero temperatures using A. forsteroides. Her work showed that

the cushion peat acted as insulation protecting roots from short periods of subzero temperatures. This work was extended in this thesis by an investigation of the thermal properties of all four cushion species. A further set of experiments was established to examine the effect of different temperatures and exposure times on survival of A. forsteroides seedlings (Chapter 8).

Both the degree of morphological convergence seen in the Tasmanian bolsters and the extremely high surface temperatures reported in the literature (39° C, Salisbury and Spomer 1964) prompted an investigation into the anatomy of cushion leaves. It was hypothesized that to withstand high thermal loads at periods of restricted water access a xeromorphic anatomy would be necessary. Secondly, given the high degree of convergence seen in the morphological characters of these species, a similar degree of anatomical convergence might be seen if Mooney and Dunn 's (1970) hypothesis of limited number of biological solutions in severe environments is correct (Chapter 9).

CHAPTER 2 THE ENVIRONMENTS AND PRIMARY PRODUCTION OF BOLSTER SPECIES AT MT. FIELD NATIONAL PARK

2.1 Introduction

To date no data on growth rates of the four Tasmanian bolster species are available and presumed habitat preferences have been assumed from observational data (Kirkpatrick 1983, Kirkpatrick et al. 1985). Data from the high alpine zone of New Zealand indicate cushion plant growth rates of 120-400 g/m^2/year (Bliss and Mark 1974).

Measurement of growth rates over altitudinal and geographical gradients does allow the relative competitive abilities of different species to be assessed. If competition is a significant factor in determining cushion species distribution then it could be expected that the different cushion species have maximum growth rates at different altitudes or at sites of different soil moisture or soil nutrient conditions.

The aims of work reported here were to compare the environments, dry matter production and phenology of cushion species in a range of sites at Mt. Field in central southern Tasmania and Mt. Wellington in south eastern Tasmania.

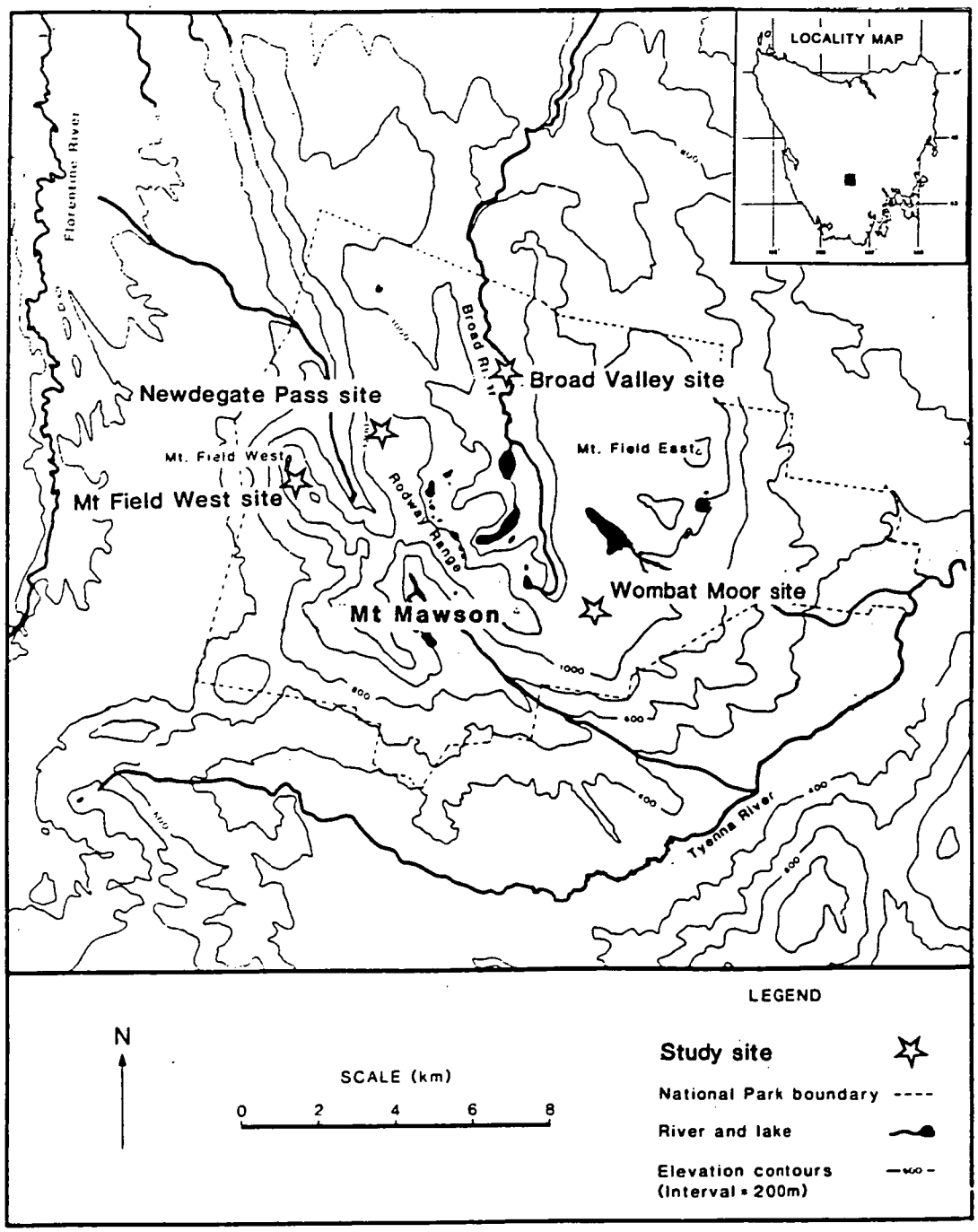
In particular it was intended to test whether -

1. there are interspecific differences in annual and seasonal above ground biomass production .
2. there are differences in above ground biomass production and reproductive success within and between species over an altitudinal gradient.
3. there are significant differences in annual and seasonal soil moisture conditions between sites dominated by the different species.
4. there are significant differences in the soil nutrient levels between sites dominated by the different species.

2.2 Study areas

The Mt. Field massif is situated in south central Tasmania (40^o 40' S, 146^o 35' E, figure 2-1). It is a roughly triangular fault block surrounded by the Derwent, Florentine and Tyenna Rivers. It is a plateau area formed by Jurassic

Figure 2-1. Map of the Mt. Field massif showing locations of study sites (After Minchin 1983).



dolerite. This is the common mountain form in the east of the state. The underlying Triassic, Permian and upper Carboniferous sediments rarely outcrop above 1000 m at Mt. Field.

The prevailing westerly airflow causes a dramatic precipitation gradient across this area, from a high of 2600 mm at Mt. Mawson with a linear decrease to 1550 mm at Lake Fenton, some 3 km east (Minchin 1983). No data are available for the alpine areas west of Mt. Mawson. The tree line occurs at approximately 1200 m in this area (Kirkpatrick 1982). Snow is most frequent in late winter and spring but can fall at any time of the year. While snowfalls and persistence are highly variable, periods of snowlie longer than a few weeks are rare, except in a few small snow patches. No long term temperature data are available. Short term maximum and minimum data indicate extremes of -4° and 38° C at 980 m and -2° and 30° C at 1300 m during the summer of 1981/82 (Minchin 1983).

Four study sites were established at Mt. Field to sample over the full altitudinal range of all four species (table 2-1). The Broad Valley and Wombat Moor sites were single species sites. At Newdegate Pass D. minimum occurred as both individual cushions or as extensive mats while 10 m away A. forsteroides and D. novae-zelandiae occurred as individual cushions and an intermixed mosaic down a steep creek line. The Mt. Field West plateau site consisted of four subsites, the most widely separated of which were 300 m apart. These subsites were established in order to sample a monospecific stand of each species. This was considered desirable in order to attempt to elucidate environmental factors determining the distribution of each species. (This was not completely possible at the Newdegate Pass site due to the restricted distribution of A. forsteroides).

Mt. Wellington is situated in south eastern Tasmania (42° 59' S, 147° 14' E) some 10 km from the sea (figure 2-2). It is a dolerite capped plateau reaching 1250 m altitude. The monthly mean maximum and minimum temperatures and precipitation based on a 10 year record are shown in figure 2-3. More recent data suggest that mean annual rainfall is of the order of 1200 mm (see figure 8 in Gibson and Kirkpatrick 1985a). Snow is generally both less frequent and less persistent than at Mt. Field. Trees occur almost to the summit on well drained sites. Some of the poorly drained ground is dominated by cushion heath. A study site was established in the Abrotanella cushion heath community on the low lying Dead Island plain (1170 m).

Table 2-1 Study sites at Mt. Field and Mt. Wellington.

SITE	ALTITUDE	SPECIES	ASSOCIATION
Mt. Field West	1400 m	(a) Donatia novae-zelandiae	Fire damaged mosaic cushion heath
		(b) Abrotanella forsteroides	Fire damaged Abrotanella cushion heath
		(c) Dracophyllum minimum	High mountain cushion heath
		(d) Phyllachne colensoi	High mountain cushion heath
Newdegate Pass	1300 m	(a) Donatia novae-zelandiae	Fire damaged mosaic cushion heath
		(b) Abrotanella forsteroides	Fire damaged mosaic cushion heath
		(c) Dracophyllum minimum	Mosaic cushion heath
Wombat Moor	1070 m	Abrotanella forsteroides	Abrotanella cushion heath
Broad Valley	830 m	Donatia novae-zelandiae	Donatia cushion heath
Mt. Wellington	1170 m	Abrotanella forsteroides	Abrotanella cushion heath

Growth studies on Mt. Field West were undertaken in pure stands of each species spread over approximately 300 m across the plateau.

Figure 2-2. Map of the location of the Mt. Wellington study site.

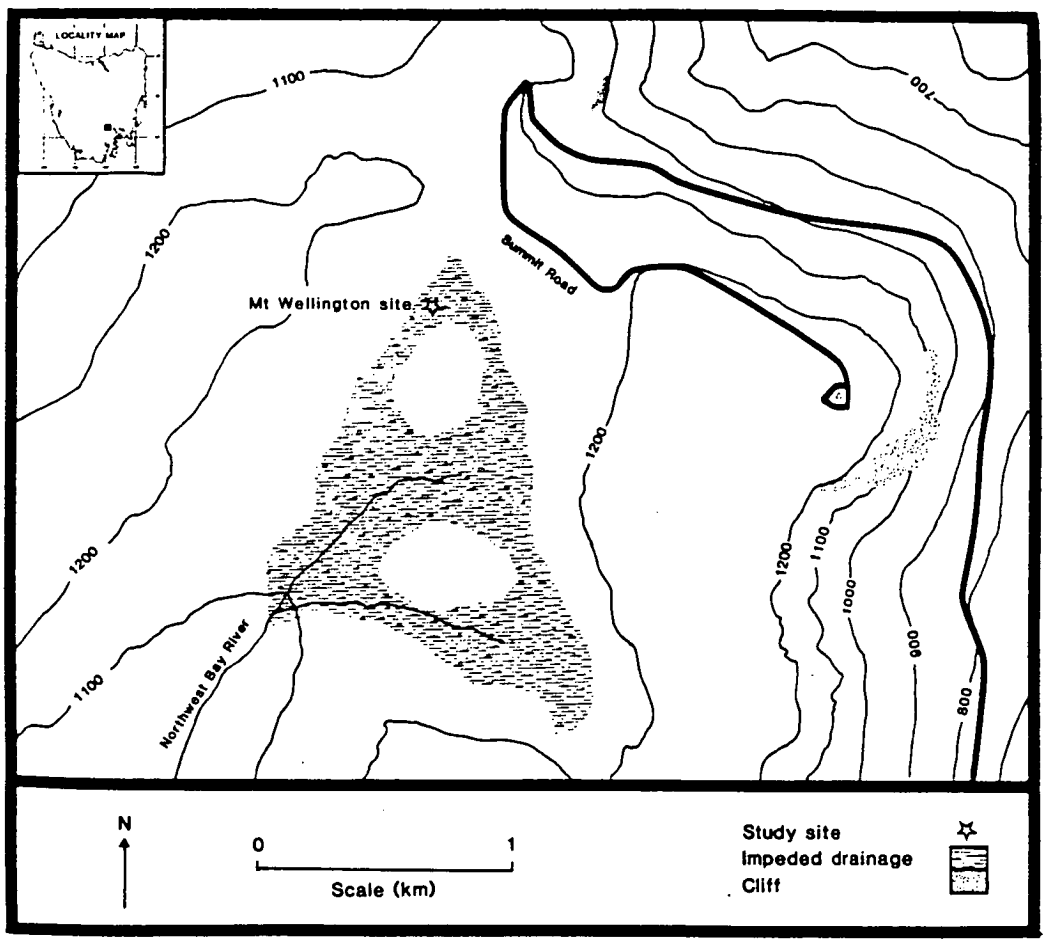
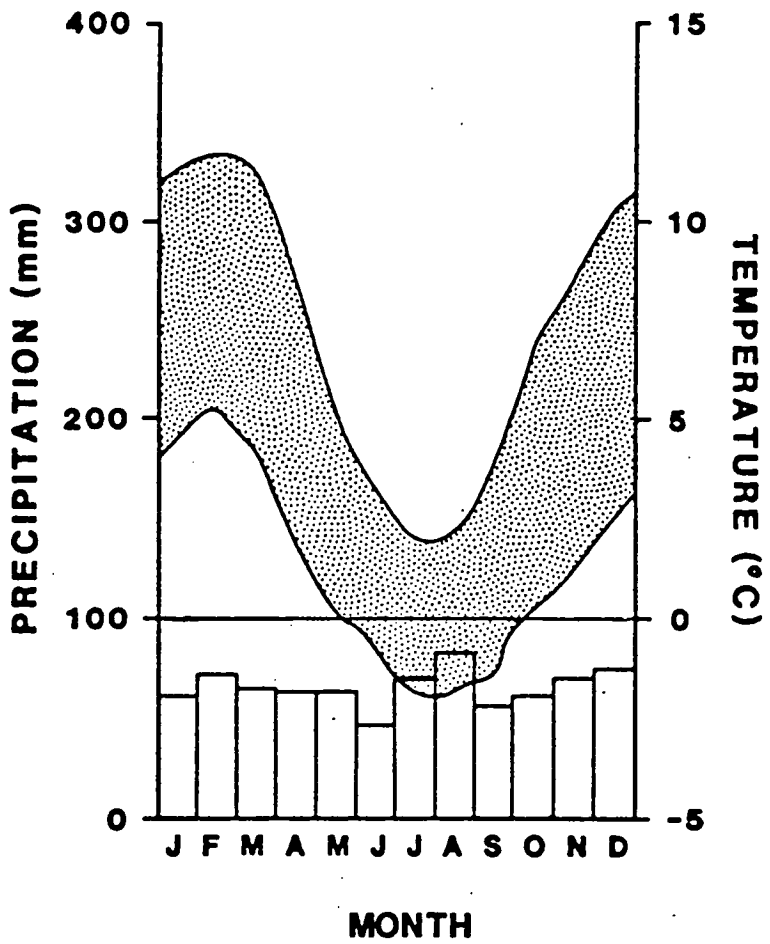


Figure 2-3. Ten year mean monthly rainfall and mean daily maximum and minimum temperature data from Mt. Wellington (After Kirkpatrick 1983).



2.3 Methods

2.3.1 The Environment

At each site a shielded maximum and minimum thermometer and a rain gauge were installed. Additional thermometers were set up on the Mt. Field West plateau where subsites were more widely separated. Each thermometer had been independently calibrated against a standard. The rain gauges were 27 cm diameter, except for the Mt. Wellington site where a 10 cm diameter gauge was used. The larger diameter rain gauges were installed at Mt. Field, in an attempt to counteract the affect of high winds (Minchin 1983).

The rain gauges and thermometers were read monthly from October 1982 to September 1984. At the same time soil temperature profiles were taken at -10, -20, -30 and -50 cm or to the underlying inorganic substrate using a digital readout transistor temperature probe. These profiles were taken from the same location each month.

Three bulked soil samples (approx. 200 g) were taken each month at 0-5 cm, 5-10 cm, and 10-20 cm depths from random locations within 5 m of the growth plots. The bulked samples were stored in screw top aluminium cans and were normally processed within 48 hours of collection. When this was not possible they were stored at 4° C until processed (always within 4 days of collection). Soil moisture determinations were made by oven drying at 105° C for a minimum of 24 hours. Water retention curves were determined for each site using the filter paper method described by Hamblin (1981).

Soil nutrient analysis was undertaken using a bulked soil sample (0-10 cm depth) from each site by the Tasmanian Government Analyst. Nitrogen content was determined by Kjeldahl digestion for both total and water soluble components. Analysis of total phosphorus was by the vanado-molybdate method on a digest of 1 g of sample with HNO_3 /$HClO_4$. Absorption was read at 400 nm on a Varian Superscan spectrophotometer. Available phosphorus was determined by Truog extract using acidified ammonium sulphate. Potassium and sodium were determined by flame emission measurement of the above digest, on an EEL flame photometer. Calcium was measured photometrically as for potassium and sodium, by dilution (1:1) of the digest with $LaCl_3$ solution.

Organic matter was measured by loss on ignition at 600° C of replicated samples from 0-5 cm and 5-10 cm depth at each site. pH was determined using a CSIRO soil testing kit. Bulk densities were determined from ten replicated 40 cc air dried soil samples from each site.

During the second year of the study, four 3-channel temperature integrators were built. These instruments are similar to those described by Hodgkinson et al. (1982) and measured total elapsed time in each of eight temperature intervals (-5° to 0° C, 0° to 5° C, 5° to 10° C, 10° to 15° C, 15° to 20° C, 20° to 25° C, 25° to 30° C, >30° C). Sensors were located immediately below the cushion surface (c. -0.5 cm), -7.5 cm in the cushion and -7.5 cm into adjacent soil. They were deployed as they became available (Mt. Field West, Aug 1983 - Sept 1984; Mt. Wellington, Dec 1983 - Sept 1984; Wombat Moor, April - Sept 1984; Broad Valley, May - Sept 1984). Monthly error between measured and elapsed time was always less than 8% and generally between 1-3%. The transistor sensors had an accuracy of + 0.05° C and a hysteresis of <0.1° C. The 0° C switch point was set at +0.2° C. This temperature was selected to avoid overestimation of the time spent in an unfrozen state at 0° C (due to latent heat properties). These instruments sampled the environment for one minute in every ten.

2.3.2 Net primary production and phenology.

Very slow growth and the absence of overwintering buds make the determination of annual growth rates of cushion plants difficult (Bliss and Mark 1974). The method adopted here was similar to that used by Bliss and Mark (1974) for New Zealand cushion plants. In late October the tip of the last fully expanded leaf was clipped on five shoots, on each of 10 cushions, of all species occurring at each site. The clipped shoots were marked with toothpicks. Growth was scored twice yearly, in late April (covering the period October -April referred to here as 'summer' growth) and in late October (covering the period April-October referred to here as 'winter' growth).

Several other methods of marking individual shoots were tried but proved less than successful. Both paint and nail varnish were initially used to mark shoots so as to inflict as little damage as possible to the shoot. However due to the waxy cuticle and large diurnal temperature fluctuations this generally lasted no more than a week. Next an attempt was made to tie fine thread about the last fully

expanded leaf. This method was abandoned due to the very small nature of the leaves.

For each cushion from which growth data were collected, the stem density in ten 5 cm x 5 cm quadrats was measured. For each species at each site three randomly chosen 5 cm x 5 cm blocks were removed to the laboratory. From each of these blocks length, number of live leaves and mean leaf dry weights were determined from ten samples dried at 90° C to constant weight. These data allowed net above ground photosynthetic standing crop and net shoot dry matter increase to be calculated for each cushion using the formulae:

Above ground photosynthetic standing crop = mean density of shoots x mean number of green leaves per shoot x mean site leaf weight. (in mg/25 cm^2).

Biomass increase = mean density of shoots x mean number of new leaves per shoot x mean site leaf weight. (in mg/25 cm^2).

Not all species occurred at all sites and the accuracy of the A. forsteroides growth data for the first summer was poor. This resulted from leaf tip morphology and the marking system used. Because of the hyaline leaf tip, the scar left by leaf clipping was difficult to relocate. Added to this the shoots were initially marked by a single toothpick which proved inadequate for accurate relocation. These problems were corrected on subsequent samplings.

Due to the nonorthogonal nature of the data, two-way analysis of variance was not possible. The data were compared using means and calculating 95% confidence limits based on pooled standard deviations.

Annual turnover rate of photosynthetic above ground standing crop was calculated by dividing the photosynthetic above ground standing crop by the annual above ground production.

Over the 1982/83 summer, flower and fruit density were measured for five 5 cm x 5 cm quadrats for each of 10 cushions of D. novae-zelandiae, P. colensoi and D. minimum at the sites where they occurred. Mean flower weight and mean seed production were estimated from 10 replicates of 10 flowers per site. Phenologies of the species were recorded at each of the monthly visits.

Given the fragile and restricted nature of these plant communities the sampling of neither the total above ground standing crop nor root biomass was permissible.

2.4 Results and Discussion

2.4.1 The Environment

Because the Newdegate Pass site was located in a south westerly facing gully (direction of the prevailing winds) the rainfall data from this site are considered unreliable. The temperature data and soil temperature profiles closely follow the Mt. Field West data (within 2^{o} C) and will not be discussed further. The additional temperature data and soil temperature profiles collected at the subsites on the Mt. Field West plateau were virtually identical and only data from the main site are presented here.

2.4.1.1 Temperature data

It was found that soil temperatures at depths of -30 cm and -50 cm on Mt. Wellington were highly correlated with the long term mean monthly temperature.

Mean monthly temperature = 0.896 (soil temperature at 30 cm) - 1.166
(R_{24} = 0.898 $P<0.001$)

Mean monthly temperature = 1.021 (soil temperature at 50 cm) - 1.938
(R_{22} = 0.949 $P<0.001$)

The mean monthly soil temperature at -30 cm was subsequently used at all sites as an estimate of mean monthly temperature since some soil profiles were less than 50 cm deep.

The extreme monthly maximum and minimum air temperature and soil temperature at -30 cm are shown in figure 2-4 for the Mt. Field West, Wombat Moor, Broad Valley and Mt. Wellington sites. The Mt. Field West site (1400 m) has a consistently lower estimated mean monthly temperature than all other sites, and the Broad Valley site (830 m) has the highest. The Wombat Moor site (1050 m) and the Mt. Wellington site (1170 m) have similar temperatures.

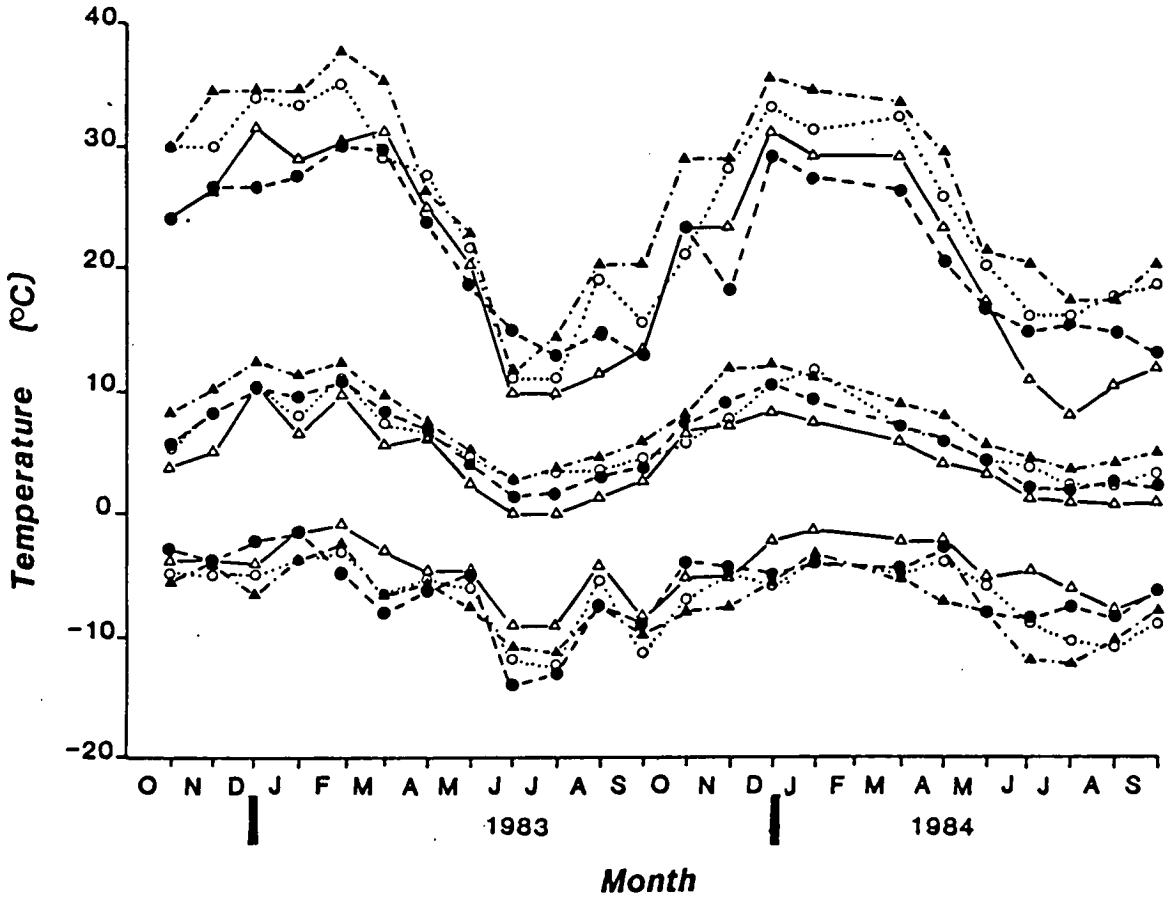


Figure 2-4. Extreme monthly maximum (upper curves) and minimum (lower curves) air temperatures at 10 cm and soil temperatures at -30 cm (which estimates mean monthly temperature - middle curves) for the four major study sites.

△—△ Mt. Field West
○···○ Wombat Moor
▲-·-▲ Broad Valley
●--● Mt. Wellington

The extreme temperatures show an interesting reversal. The Broad Valley site generally shows the highest extreme temperatures, and recorded the lowest extreme temperatures on 40% of occasions. The Mt. Field West site usually had the highest monthly extreme minimum. Mt. Field West is an isolated high plateau on which extreme minimum temperatures are a result of the passage of cold fronts and long wave reradiation. The Broad Valley, and to a lesser degree, the Wombat Moor and the Mt. Wellington sites are subject to cold air drainage. Thus the Broad Valley site has both the highest estimated mean monthly temperatures and also the largest temperature variation.

The more maritime climate expected on Mt. Wellington (1170 m, 10 km from the sea) is only partially apparent. Mt. Wellington experiences a lower extreme maximum temperature than Wombat Moor and a similar estimated monthly mean temperature. However it experienced colder extreme maximum temperatures on 30% of occasions. This is contrary to the expected ameliorating effect of proximity to the sea. This anomaly might result from differences in snowlie between the two sites. Mt. Wellington experiences less snowlie than Wombat Moor with the result that the minimum thermometer on Mt. Wellington is likely to be exposed to the air for more time than the one at Wombat Moor. (Thermometers were set 10 cm above the ground).

There were large differences in the climate of the sites between the two years of this study (figure 2-4). The summer of 1982/83 had a heavy snow fall (approx 10 cm) in January. This is reflected in the lower estimated mean temperature and a depressed extreme maximum temperature recorded during January. The onset of cooler weather was rapid after February of 1983 while the onset was delayed in 1984 and not as rapid. The summer of 1983/84 did not include a cold snap. The estimated mean monthly temperatures of the winter of 1984 were approx. 1-2^{o} C warmer than the previous year.

2.4.1.2 Rainfall data

Rainfall data from the four sites are shown in figure 2-5 and table 2-2. Minchin (1983) estimates mean annual rainfall at Wombat Moor to be 2030 mm. In both the 1982/83 and 1983/84 measuring periods total rainfall fell well short of this figure (20-30%). Minchin (1983) also reported a strong east-west precipitation gradient over 3 km from Lake Fenton across Wombat

Figure 2-5. Monthly rainfall data from the four study sites; a. Mt. Field West, b. Wombat Moor, c. Broad Valley, d. Mt. Wellington. (Dark bars indicate pooled data, zero readings resulted from broken gauges.)

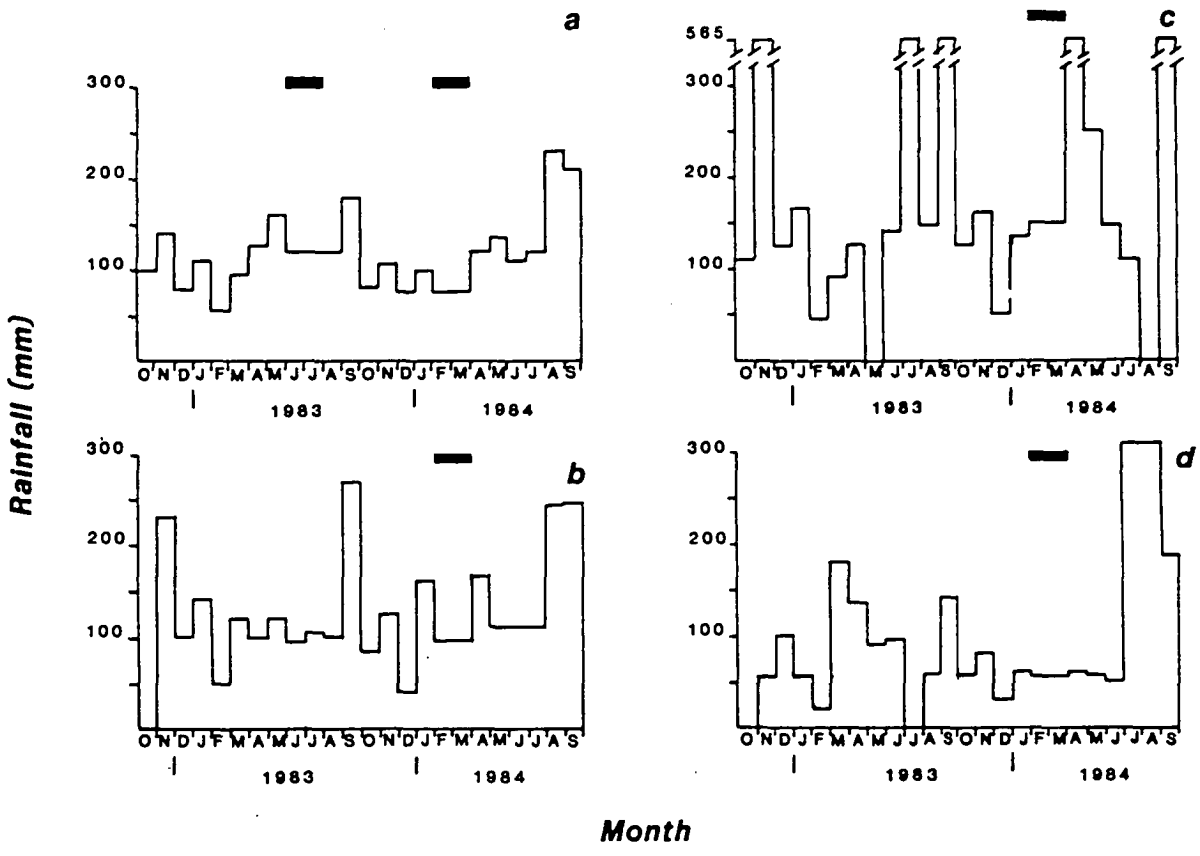


Table 2-2 Annual precipitation recorded over a two year period (+ indicates that rainfall exceeded gauge capacity at least twice).

	Oct 82 - Sept 83	Oct 83 - Sept 84
Mt. Field West	1400	1430
Wombat Moor	1440	1580
Broad Valley	2640+	2450+
Mt. Wellington	920	1290+

Moor to Mt. Mawson (figure 2-1). No such gradient was found between Wombat Moor and Mt. Field West (some 5 km further west). Indeed the rainfall patterns appear much more complex than suggested by Minchin (1983). In both years Wombat Moor had the higher annual rainfall. Even more surprising was the extremely high rainfall figures recorded in the Broad Valley (figure 2-5). Monthly rainfall exceeded 565 mm (capacity of the rain gauge) on five occasions in 24 months. The Broad Valley site recorded 40-50% more rainfall than Mt. Field West.

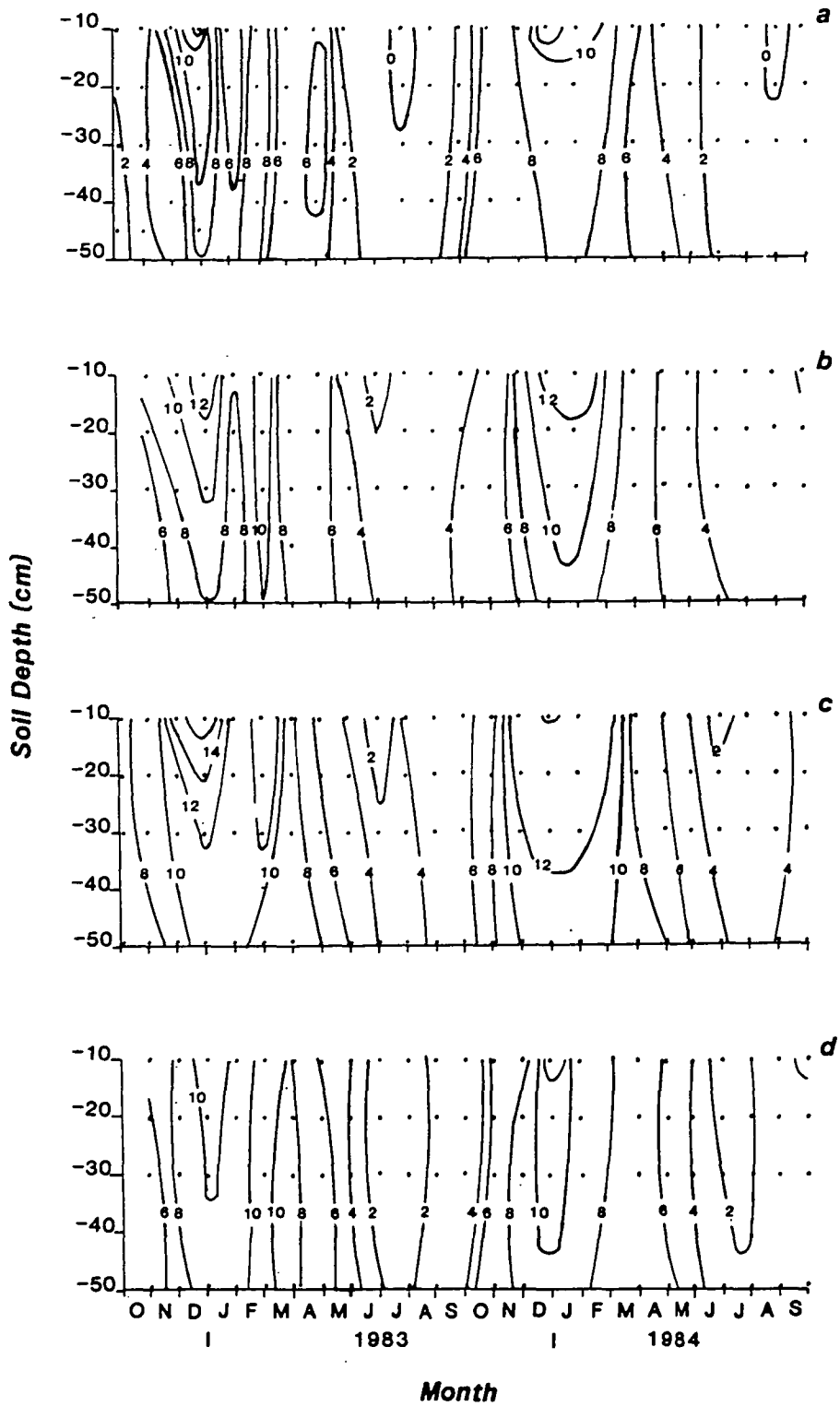
Measuring rainfall in areas subjected to strong winds is always difficult (Griffiths and McSaveney 1983). It may be that the rainfall figures from the Mt. Field West, Wombat Moor and Mt. Wellington sites which are all subjected to driving south westerly gales, underestimate actual precipitation due to a large horizontal component in the rain. The Broad Valley is a very sheltered site and most rain falls vertically. Precipitation which falls as snow could also be expected to be undersampled. The Mt. Field West and Wombat Moor sites show a similar overall rainfall pattern. The driest month at all sites occurred in February of 1983. The Broad Valley showed a more variable rainfall pattern. The rainfall pattern on Mt. Wellington was similar to Mt. Field West and Wombat Moor but although still fairly evenly distributed, total rainfall was considerably lower. No month at Mt. Field recorded less than 40 mm while the lowest recording on Mt. Wellington was 20 mm. Rainfall on Mt. Wellington, Mt. Field West and Wombat Moor appeared to have a variable peak in spring - early summer, while peak rainfall in the Broad Valley was more variable.

2.4.1.3 Soil temperature profiles

The soil temperature profiles (figure 2-6) show energy input being correlated with altitude. The highest energy input occurred at the Broad Valley site (830 m) and the lowest at the Mt. Field West site (1400 m). During January of 1983 there was a prolonged cold snap with snowfall on higher sites. All profiles show a temporary drop in soil temperatures at that time. The summer of 1983/84 showed no such occurrence and total energy input was considerably greater at all sites.

Only on Mt. Field West did soil freezing occur. In 1983 this occurred in July while in 1984 it occurred in August. On both occasions the soil remained frozen for less than a month and only to depths slightly greater than 20 cm.

Figure 2-6. Soil temperature profiles from; a. Mt. Field West, b. Wombat Moor, c. Broad Valley, d. Mt. Wellington. Dots indicate depth and time of sampling.



Except for the temperature reversal in summer of 1982/83, the pattern between years was similar but temporal variability in the onset of the cooling and warming phases is apparent.

Data from the Mt. Wellington site show a more variable energy input than Wombat Moor. Soil temperatures range from 2^{o} to 10^{o} C at 50 cm on Mt. Wellington but only 4^{o} to 8^{o} C at Wombat Moor over the two years. It was expected, due to the proximity of the sea, that Mt. Wellington might have a more equable climate than Wombat Moor. However this was not found to be the case. The lower than expected temperatures at Wombat Moor may have resulted from longer periods of snowlie. Monthly trips did not allow measurement of the period of snowlie to be made.

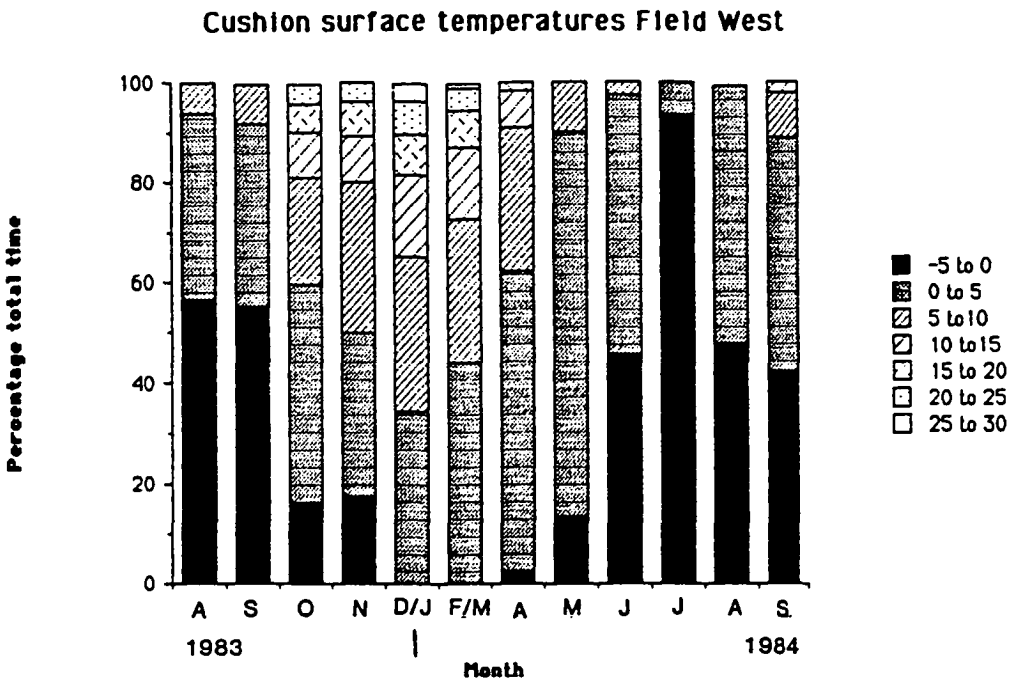
2.4.1.4 Temperature integrator data

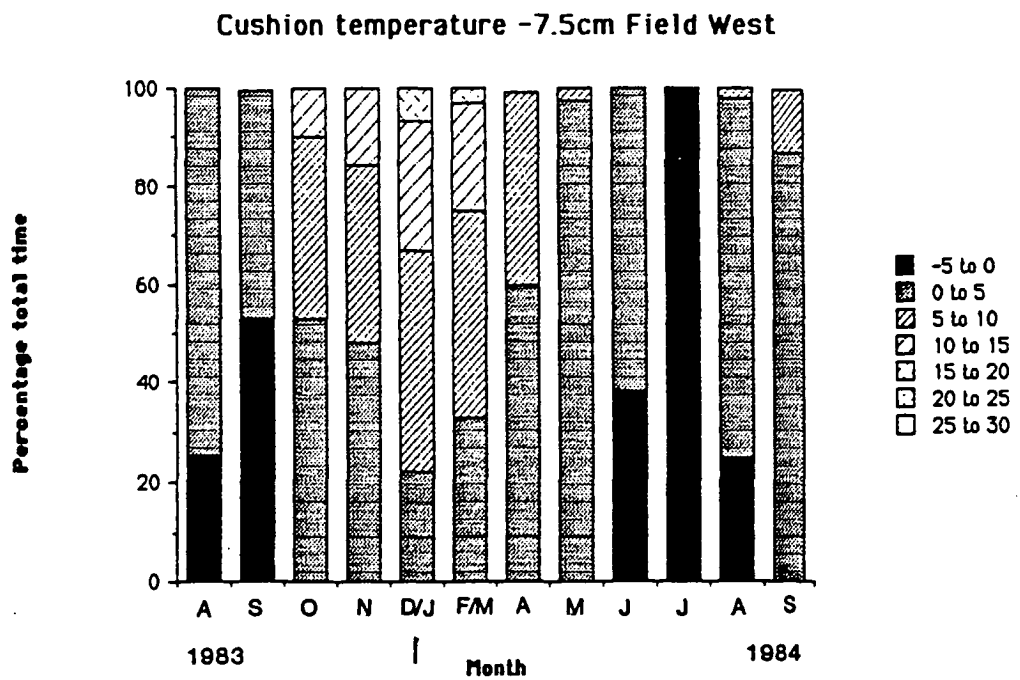
Integrated temperature data are available for 14 months from the Mt. Field West site; 10 months from the Mt. Wellington site; six months from the Wombat Moor site and five months from the Broad Valley site (figure 2-7). Time spent in each of eight temperature intervals was measured immediately below the cushion surface and at -7.5 cm into the cushion and into adjacent soil. These latter two measurements produced virtually identical results and only the results from the probe -7.5 cm into the cushion will be considered here. On both Mt. Field West and Mt. Wellington measurements were made bimonthly between December 1983 - March 1984 due to field work commitments in New Zealand.

On Mt. Field West, energy input reached its maximum during December/January 1984 and its minimum during July 1984, both on the cushion surface and at depth. Mt. Wellington showed similar trends.

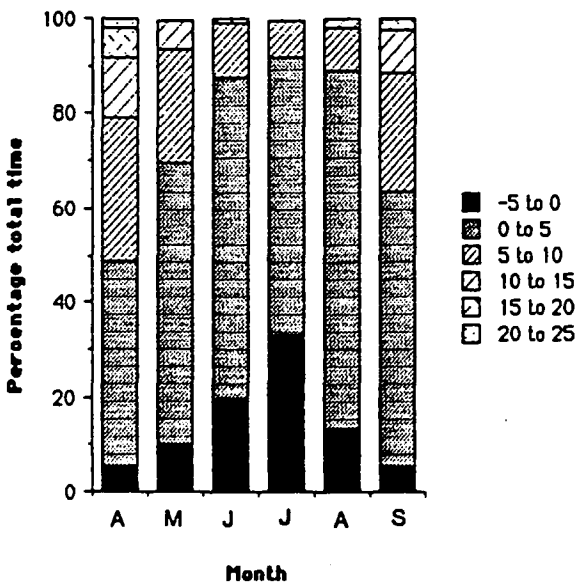
It is also apparent from the data that the cushions were achieving temperatures well above ambient by the absorption of radiation. For example, at Mt. Field during December/January 1984 cushion surface spent 10% of the total time at temperatures of greater than 20^{o} C, while extreme maximum air temperature over this period was only 31^{o} C. If cushion temperatures were not rising significantly above ambient temperature this would imply ambient

Figure 2-7. Monthly integrated temperature data from Mt. Field West, Mt. Wellington, Wombat Moor and Broad Valley showing temperatures at cushion surfaces and at depths of 7.5 cm into cushions.

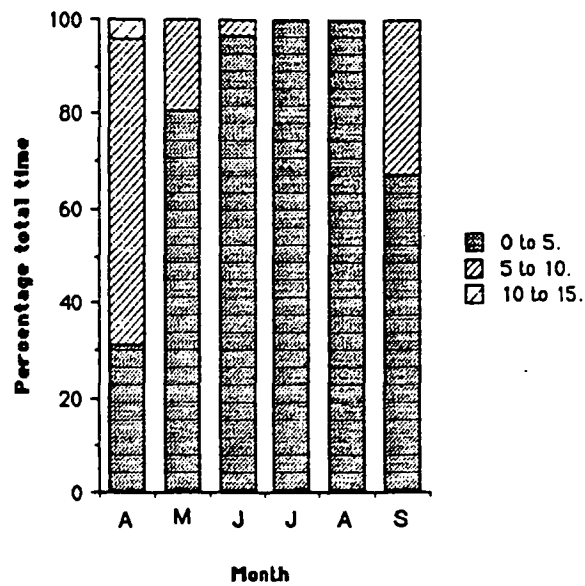




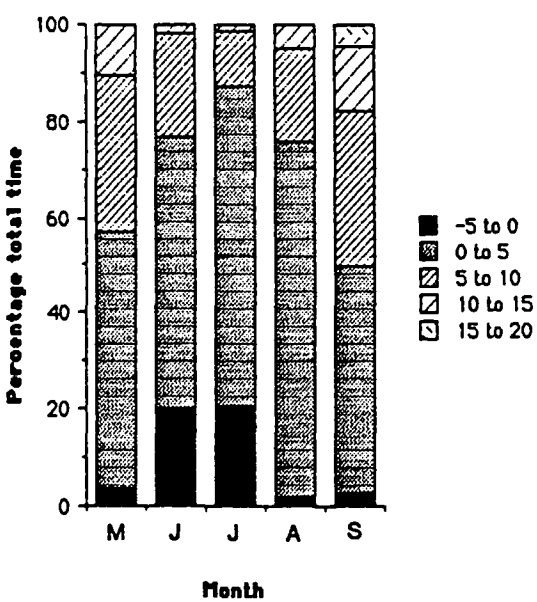
Cushion surface temp Wombat Moor



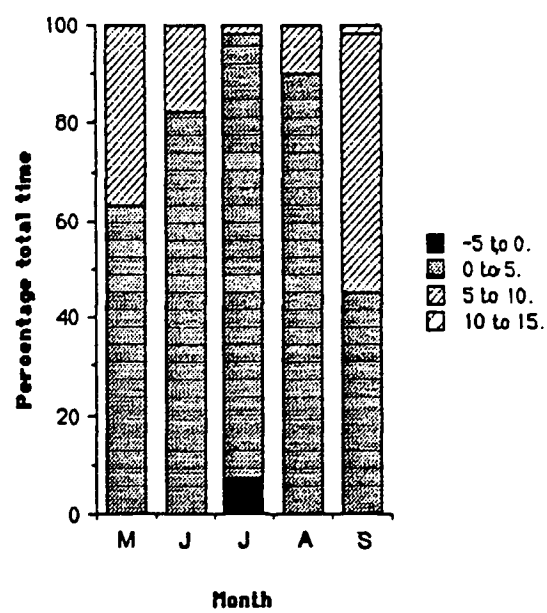
Cushion temperature -7.5cm Wombat Moor



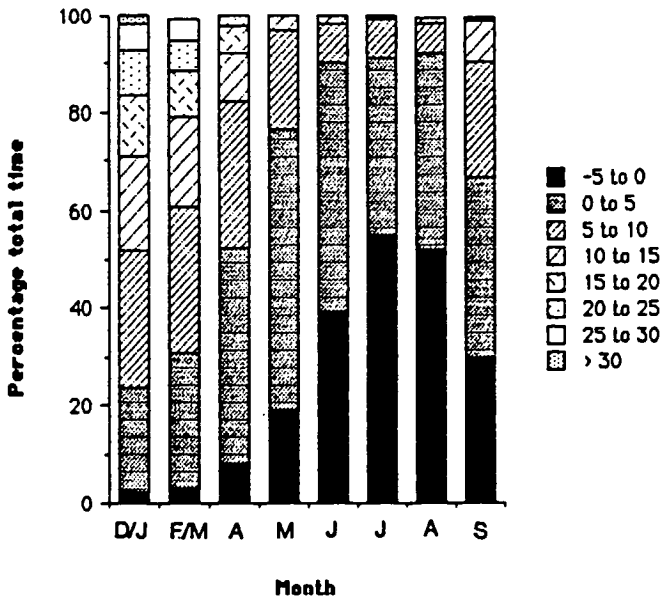
Cushion surface temperature Broad Valley



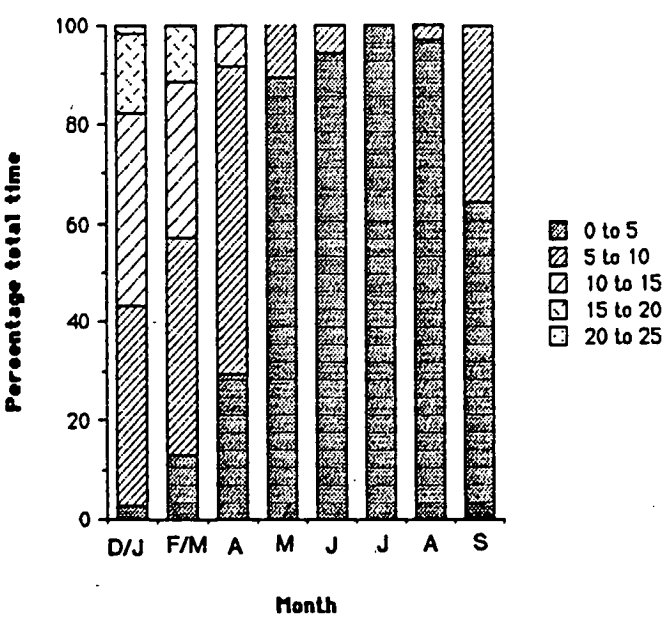
Cushion temperature -7.5cm Broad Valley



Cushion surface temperature Wellington



Cushion temperature -7.5cm Wellington



temperatures of more than 20° C for an average of 2.4 hours per day. This is extremely unlikely.

Likewise in October 1983 cushion surface temperature was greater than 20° C for 5% of the time, while the extreme maximum temperature was only 23° C. Similar results were found on Mt. Wellington. In December/January 1984, 16% of the time was spent at temperatures greater than 20° C while the extreme maximum reached only 29° C.

Mt. Field West showed less total energy input than Mt. Wellington at all times of the year. This was especially apparent over the winter months. Energy input was considerably dampened at -7.5 cm during the summer but was similar to surface values over the winter. The Broad Valley experienced the highest input of energy over winter. The temperature data from the Wombat Moor site was again less variable than those from Mt. Wellington.

The close correlation between the soil temperature data and the probe at 7.5 cm depth in the cushion at the various sites indicates that the peat soils have similar thermal characteristics to the peats produced by the cushions. This will be discussed further in chapter 8.

2.4.1.5 Soil moisture data

Using the method of Hamblin (1981) soil moisture retention curves were determined for each site (Appendix 2). An inspection of field data and these curves showed that only the soils near the D. minimum on Mt. Field West ever dropped below field capacity. This soil did so for only one month. Most soils were usually saturated with free standing surface water, except for the soils of the P. colensoi and D. minimum subsites on Mt. Field West (table 2-3).

2.4.1.6 Soil nutrient analysis

The soil analysis showed a low pH and a high percentage of organic matter at all sites (table 2-4). The soil with the lowest organic matter content was found on Wombat Moor but this is probably an artifact caused by higher surface flows following the redirection of drainage lines for water storage. The better drained soils of D. minimum and P. colensoi subsites on Mt. Field West had a lower organic matter content than the remaining sites.

Table 2-3 Percentage of time soil moisture was above field capacity and saturation (free water).

SITE	% time above field capacity	% time at saturation
Mt. Field West		
Donatia	100	50
Dracophyllum	96	21
Abrotanella	100	58
Phyllachne	100	29
Newdegate		
Dracophyllum/ Abrotanella/Donatia	100	42
Wombat Moor		
Abrotanella	100	58
Broad Valley		
Donatia	100	42
Mt. Wellington		
Abrotanella	100	71

Table 2-4 Soil analysis from cushion dominant vegetation. Single analysis from 5 bulked samples at each site.

	SITES							
	FIELD WEST				NEWDEGATE	WOMBAT	BROAD	MT.
	Donatia	Dracophyllum	Abrotanella	Phyllachne	PASS	MOOR	VALLEY	WELLINGTON
pH	3.5	4.0	3.5	4.0	3.5	3.5	4.0	3.5
Bulk Density (g/cc)	0.41	0.44	0.39	0.55	0.47	0.53	0.29	0.36
Organic Matter (%) (0-10 cm)	85	40	68	44	55	34	66	72
Available P (ppm)	<3	14	9	6	9	n.d.	5	8
Total P (ppm)	269	210	219	300	328	118	386	203
Soluble N (ppm)	87	128	95	87	138	80	120	135
K (ppm)	75	238	63	125	113	75	125	88
Na (ppm)	50	50	38	75	63	88	100	63
Ca (ppm)	650	350	325	875	1125	275	375	225
Total N (%)	1.5	0.9	1.8	0.7	1.4	0.8	1.6	1.2

All sites had similar soil nutrient levels (with the exception of calcium), with particularly low values of available phosphorus and soluble nitrogen. Bowden (1979) reports median soil values of 800 ppm for phosphorus, 2000 ppm for nitrogen, 14000 ppm for potassium, 500 ppm for sodium and 15000 ppm for calcium. The pool of available nutrients in these highly acid and usually water logged soils is therefore extremely low and is likely to severely limit dry matter production. The variation in calcium levels is not likely to have a significant influence on plant growth, given that even the highest concentrations recorded are very low compared with normal soil calcium levels.

2.4.2 Net primary production and phenology

2.4.2.1 Growth data

Data on growth of A. forsteroides leaves over the 1982/83 summer period were badly underestimated (see pg. 17). As a result the data obtained indicate minimum values only. This species was therefore excluded from data analysis for this period.

The photosynthetic standing crop, shoot density, summer, winter, and annual leaf production and leaf turnover rates for 1982/83 and 1983/84 are shown in table 2-5. A. forsteroides has consistently the highest shoot density followed by D. minimum, P. colensoi and D. novae-zelandiae. There were no significant differences in density between sites for D. novae-zelandiae and D. minimum. The shoot density of A. forsteroides at Newdegate Pass was significantly higher than all other species at all sites.

There were highly significant differences in total leaf production between species over the two year period (figure 2-8). However for the three species for which data are available there were no significant site differences between the years, except for D. novae-zelandiae at Newdegate Pass. D. novae-zelandiae and D. minimum showed overall decreases in annual leaf production of 10-34% in the 1983/84 periods (figure 2-8). P. colensoi showed a very slight increase.

The ranking of D. minimum, D. novae-zelandiae and P. colensoi at both Newdegate Pass and Mt. Field West was the same in both years. However there

Table 2-5 Values for photosynthetic above ground standing crop, density, shoot elongation, turnover rate, and annual production data. Biomass data are in g/m^2, with shoot elongation in mm, and density in shoots/m^2.

SITE	Photosynthetic above ground standing crop	density	1982/83 shoot summer production	1982/83 winter production	1982/83 annual production	1982/83 shoot elongation	1982/83 turnover rate (yr)	1983/84 summer production	1983/84 winter production	1983/84 annual production	1983/84 shoot elongation	1983/84 turnover rate (yr)
MT FIELD WEST (1400 m)												
Donatia	769	56 760	314	43	357	1.1	2.15	309	13	322	1.1	2.39
Dracophyllum	656	84 640	388	63	451	0.8	1.45	331	28	359	0.7	1.83
Abrotanella	301	114 400	246*	150	396*	1.3*	0.76	492	140	632	2.2	0.48
Phyllachne	361	82 480	221	61	282	1.0	1.28	255	30	285	1.1	1.27
NEWDEGATE PASS (1300 m)												
Donatia	895	51 440	512	60	572	1.6	1.56	359	24	383	1.2	2.34
Dracophyllum	711	92 400	425	52	477	1.3	1.49	376	36	412	1.1	1.73
Abrotanella	309	137 720	288*	152	440*	1.5*	0.70	563	146	709	2.3	0.44
WOMBAT MOOR (1030 m)												
Abrotanella	232	110 160	261*	139	400*	1.3*	0.58	434	157	591	1.8	0.39
BROAD VALLEY (830 m)												
Donatia	725	60 240	379	54	433	0.8	1.67	305	74	379	0.7	1.91
MT WELLINGTON (1150 m)												
Abrotanella	183	105 200	207*	83	290*	1.0*	0.63	325	101	426	1.5	0.43

* Abrotanella measurements are minimum values.

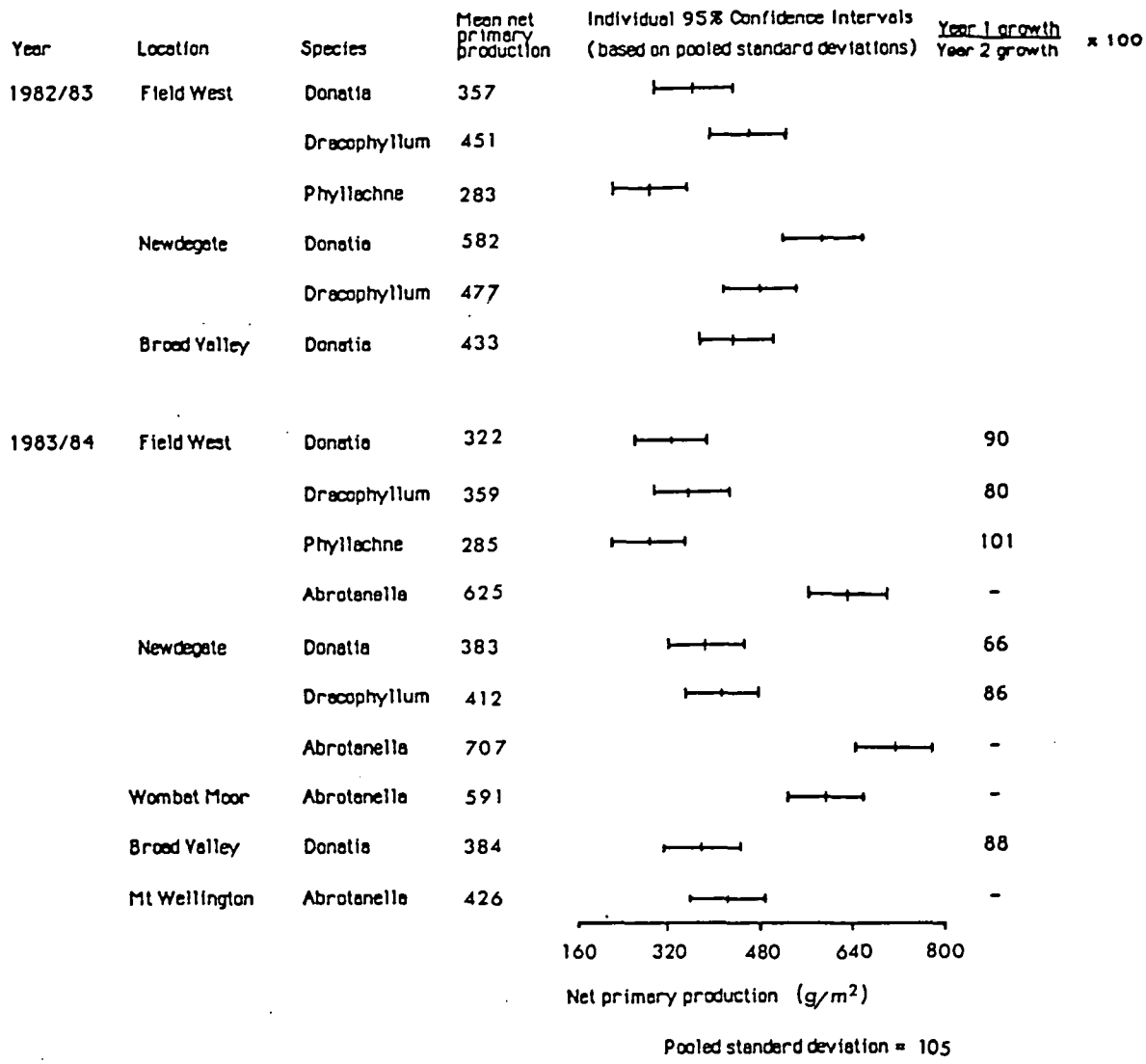


Figure 2-8. Analysis of yearly net above ground dry matter production between species, sites and years.

was no significant difference between leaf production of D. minimum and P. colensoi in the second year.

D. novae-zelandiae occurred at three sites, Mt. Field West (1400 m), Newdegate Pass (1300 m) and Broad Valley (830 m). In 1982/83 the best growth was achieved at Newdegate Pass followed by the Broad Valley and Mt. Field West. In 1983/84 the ranking was the same. However, the significant difference between the Newdegate Pass site and the other two sites had disappeared. Leaf dry matter production during 1983/84 was very similar at Broad Valley and Newdegate Pass.

In both years D. minimum achieved greater production at Newdegate Pass than at Mt. Field West. In 1983/84 A. forsteroides from Mt. Field West, Newdegate Pass and Wombat Moor was significantly more productive than all other species at all sites. The mean shoot biomass production of A. forsteroides at Mt. Wellington was also higher than other species at all sites but not significantly different. As with D. novae-zelandiae and D. minimum the highest production rate was found at the Newdegate Pass site.

Analysis of summer and winter production values show a somewhat more complicated pattern (figures 2-9, 2-10). While the overall patterns in summer growth rates are similar to that described above, the growth rates of A. forsteroides in the second year are more comparable with the other species (but still significantly greater). P. colensoi shows a 15% increase in the second summer while D. novae-zelandiae and D. minimum show decreases of between 2-30%, however these decreases are less than those of the yearly total.

Analysis of the winter shoot production shows marked differences for all species between the two years (figure 2-10). From the Mt. Field West and Newdegate Pass sites D. novae-zelandiae, D. minimum and P. colensoi show decreases in net shoot production of between 31-69%, while A. forsteroides shows a decrease of 4-7%. However net shoot production of D. novae-zelandiae from the Broad Valley increases by 37% in the second winter while A. forsteroides from Wombat Moor and Mt. Wellington show increases of 13% and 22% respectively.

The other obvious difference in shoot production over winter is the much faster growth of A. forsteroides (2.5-7 times) at Mt. Field West, Newdegate Pass and Wombat Moor compared to the other species. Indeed there is no significant

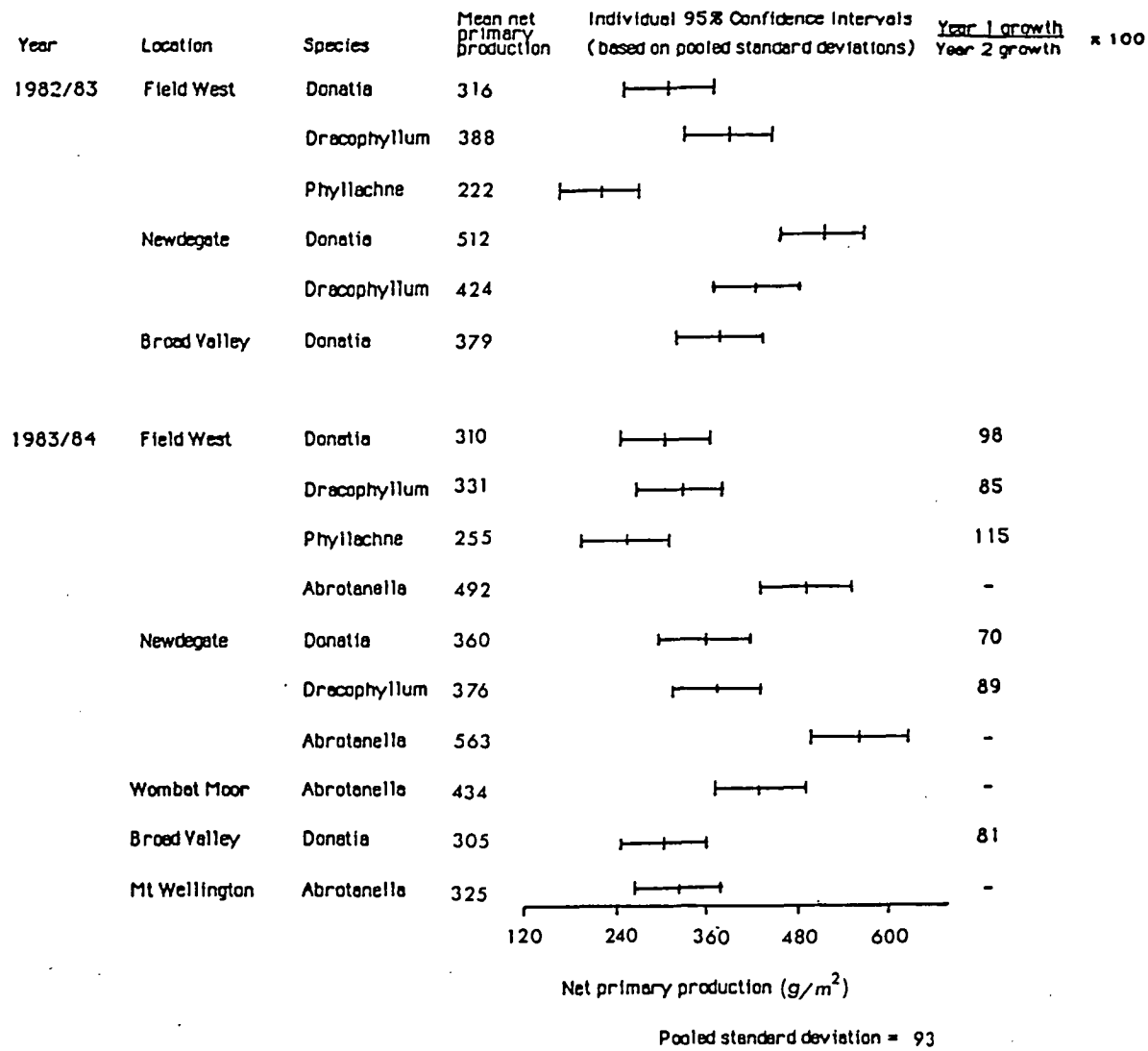


Figure 2-9. Analysis of net 'summer' (October-April) above ground dry matter production between species, sites and years.

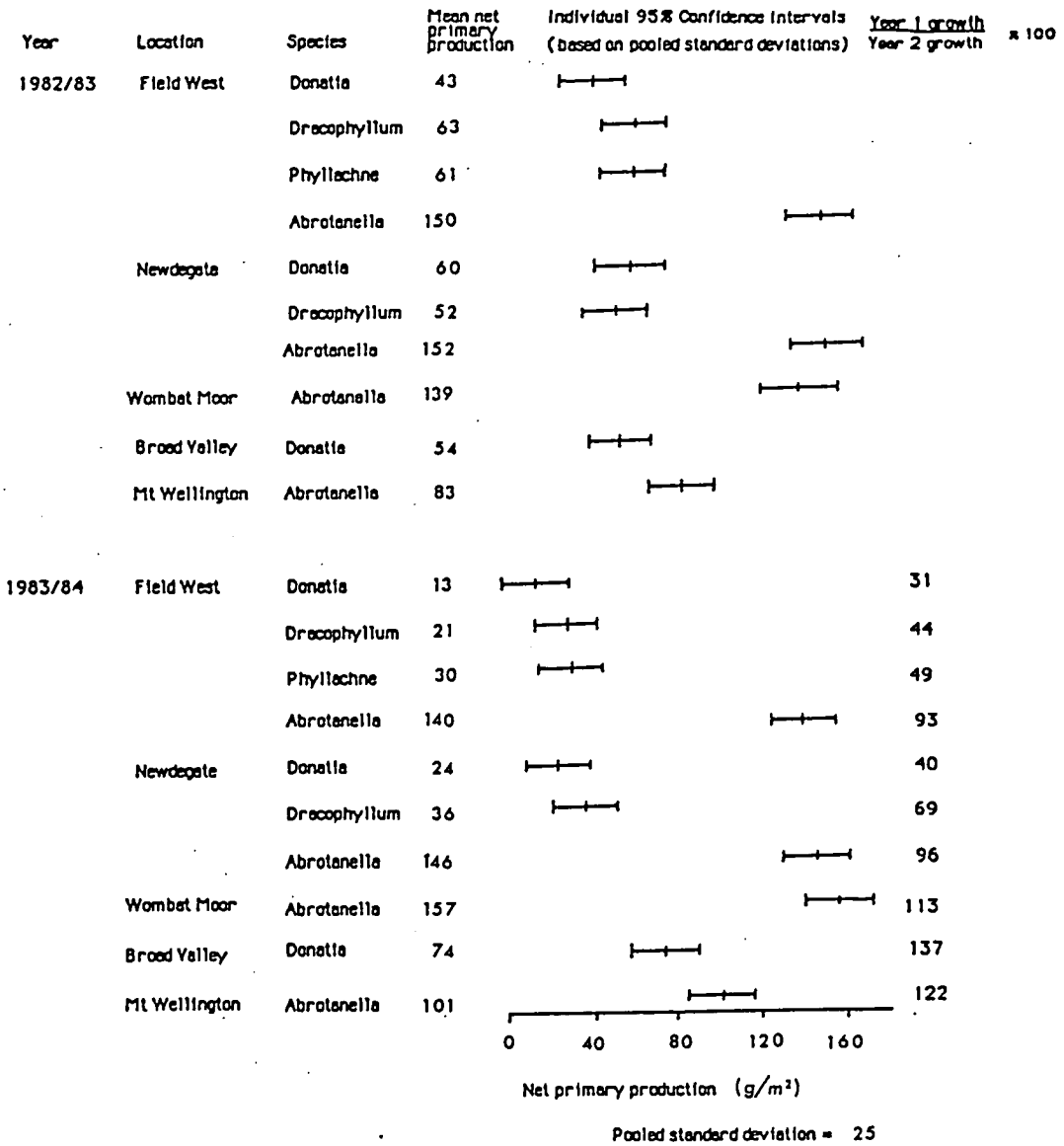


Figure 2-10. Analysis of net 'winter' (April-October) above ground dry matter production between species, sites and years.

difference in shoot production between these sites despite some 330 m altitude difference. Why A. forsteroides on Mt. Wellington did not show similar growth is unclear but may be related to soil aeration. The Mt. Wellington site had the poorest soil aeration (table 2-3) and is therefore likely to have suffered a high degree of nutrient stress given the low pH and the anaerobic conditions.

Leaf turnover rates varied quite markedly between species, with A. forsteroides having the fastest rate (leaves lasting 0.39-0.48 years,1983/84 data) and D. novae-zelandiae having the slowest (leaves lasting 1.91-2.39 years,1983/84 data - table 2-5). The quicker turnover of leaves by A. forsteroides largely reflects its faster growth rate. One suggested advantage of the evergreen shrub habit is the low maintenance costs in carbohydrate such that there is no necessity to produce new photosynthetic apparatus every year (Billings 1974b). This does not appear to hold for A. forsteroides. It has also been suggested that the older green leaves act as winter food storage organs (Hadley and Bliss 1964). This aspect of cushion plant biology was not investigated. In the northern hemisphere the leaves of most evergreen shrub species in alpine and tundra environments function for 2-4 years. The functional life of bolster species leaves is much shorter in Tasmania (5 -29 months).

2.4.2.2 Phenology

The phenology of the four cushion species over the summer of 1982/83 is shown in figure 2-11. The first buds and flowers of A. forsteroides appeared in October at all sites. The flowers of this species are minute and not easily seen until after fertilization and subsequent expansion of the peduncles has occurred. By early November all buds had opened except at the highest altitude site. The period of seed maturation appeared to be correlated with altitude; taking 2 months at Wombat Moor (1070 m) and Mt. Wellington (1170 m), 3 months at Newdegate Pass (1300 m) and 4 months on Mt. Field West (1400 m). Seed dispersal was somewhat delayed on Mt. Field West.

Dracophyllum minimum produced buds and flowers in synchrony at Newdegate Pass and Mt. Field West but again first maturation was delayed at the higher altitude. P. colensoi showed a very similar pattern to D. minimum but was noteworthy in its extremely rapid dispersal phase (1-2 weeks). Bud and flower production was approximately 2 months earlier on Mt. Field West than that reported for P. colensoi at 1390 m in New Zealand (Bliss and Mark 1974).

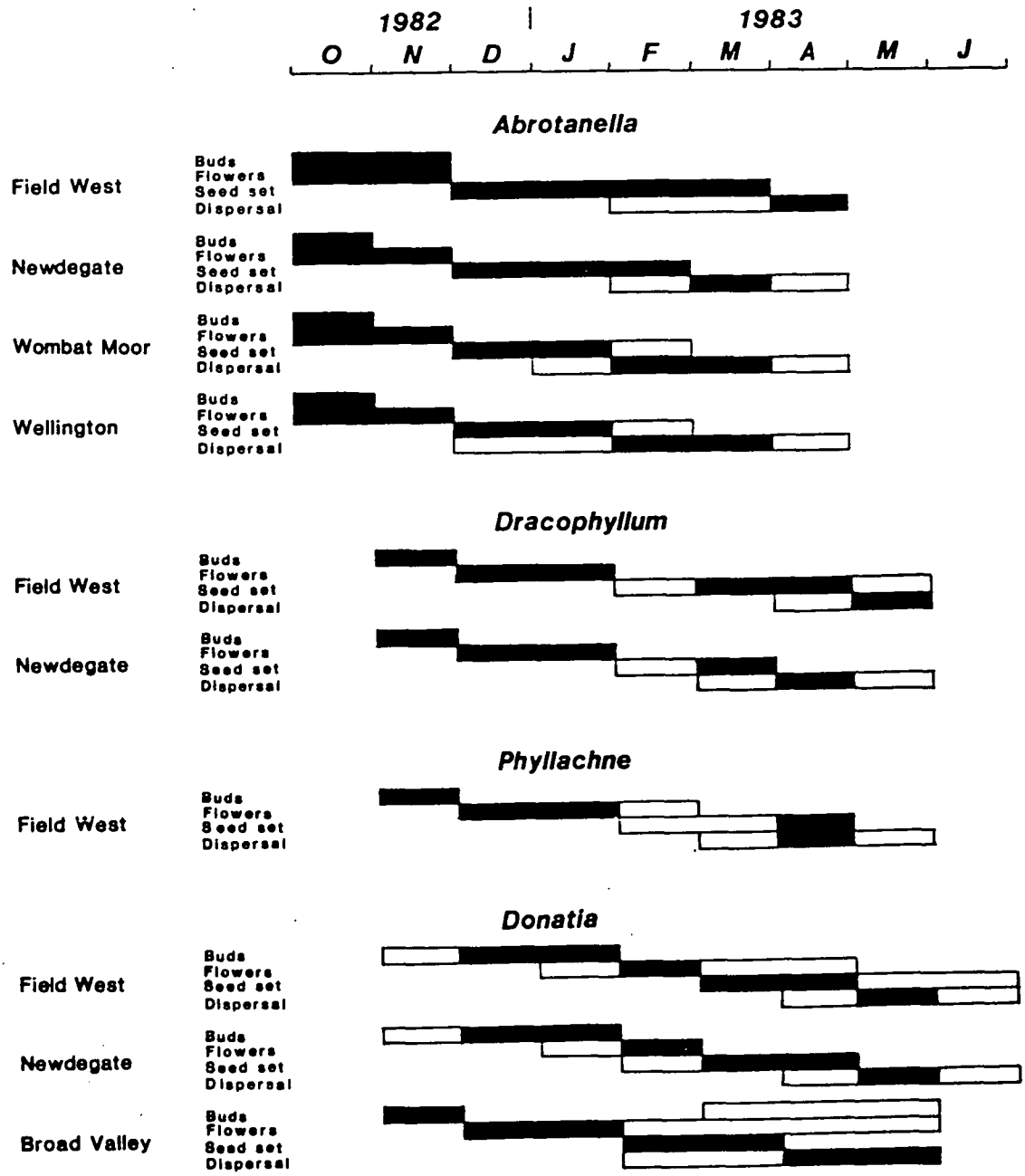


Figure 2-11. Phenology of the four cushion species shown by sites. Solid bars indicate peak times,open bars indicate non-peak period.

Donatia novae-zelandiae had the latest flowering period with most buds appearing in early December at Newdegate Pass and Mt. Field West and a month earlier in the Broad Valley. Similar patterns were seen at the two higher altitude sites while D. novae-zelandiae at the Broad Valley site showed an accelerated phenology. The phenology of all four bolster species appears dependent on temperature rather than photoperiod.

All Tasmanian bolster species initiate flower buds in the season prior to flowering as was found by Mark (1970) for most New Zealand species. Reproductive activity is thus dependent to some degree on the previous growing season. There is a predominance of small white flowers in the alpine floras of both Tasmanian and New Zealand which Primack (1978) regards as being an adaptation to a highly variable pollinator assemblage. Bliss (1971) considers the small white flowers of alpine New Zealand to be unattractive to insects with few being seen visiting them. Three of the bolster species studied (P. colensoi, D. minimum, D. novae-zelandiae) produce small white flowers with copious supplies of nectar and a strong scent. On still warm summer days the bolsters are heard before they are seen, being completely covered by insects from several different families (beetles, flies, butterflies, european bees). In contrast to the northern hemisphere flowering in the alpine areas of New Zealand and Tasmania is not synchronous.

2.4.2.3 Reproductive Biomass

The very small nature of the flowers of A. forsteroides made accurate counting impossible. Data were collected on the flower and fruit density, and number of seed set for the other three species over the 1982/83 summer (table 2-6).

P. colensoi flowered extremely prolifically during the 1982/83 season turning most of the cushions white. A very large number of nectar seeking insects were apparent; these included beetles, flies, butterflies and European bees. D. novae-zelandiae also flowered profusely on Mt. Field West but flower density declined with decreasing altitude. D. minimum flowered poorly on Mt. Field West. Very low densities were observed at Newdegate Pass, where all flowers subsequently aborted.

Table 2-6. Flower production 1982/83 summer. Values given on a square metre basis.

SITE	SUMMER 1982/83				
	flower density	flower set density	flower biomass (g)	# seed set	% annual leaf production
MT FIELD WEST (1400 m)					
Donatia	10 440	4 680	38	23 870	11
Dracophyllum	1 280	560	22	17 140	5
Phyllachne	32 600	N/A	86	N/A	30
NEWDEGATE PASS (1300 m)					
Donatia	8 800	5 720	30	38 900	5
Dracophyllum	280	0	4	0	1
BROAD VALLEY (830 m)					
Donatia	2 800	400	9	2 370	2

N/A not available

The dispersal period for P. colensoi was very short (1-2 weeks) and sampling of mature fruits was missed. Data from D. novae-zelandiae and D. minimum showed that between 0 - 39,000 seeds/m^2 were being produced by these species at Newdegate Pass and Mt. Field West. The reproductive success of the bolster species was thus highly variable, net reproductive biomass was also variable ranging from 1-11% of the annual shoot production for D. novae-zelandiae and D. minimum to at least 30% for P. colensoi.

There is no necessity for evergreen shrubs to flower every year. Indeed a high degree of variability in both flowering and reproductive success was seen both within and between the four bolster species studied. At Newdegate Pass D. minimum failed to set any seed in the summer of 1982/83 and seed production on Mt. Field West was low. By contrast P. colensoi invested a large amount of carbohydrate in reproduction that year (85 g/m^2 into reproductive structures and 282 g/m^2 into new shoot growth).

2.4.3 General discussion

The Tasmanian alpine climate appears highly variable from year to year, especially in relation to rates and onset of summer and winter cycles. The year 1983/84 had a warmer summer and a milder winter than 1982/83. In neither year was soil moisture limiting.

The annual net shoot production was variable between the two summer and winter growth periods for D. novae-zelandiae, D. minimum and P. colensoi. Over all in the milder second year of this study D. novae-zelandiae and D. minimum showed depressed shoot growth while P. colensoi showed little change.

Given the restricted high altitude distribution pattern of P. colensoi it was expected that this species might do better in winter and cooler summer periods than the other cushion species on Mt. Field West. In fact during the warmer summer of 1983/84 it showed a 15% increase in shoot production and showed both a similar winter production rate to D. minimum and D. novae-zelandiae and a similar depression in growth over the warmer winter of 1984. Overall P. colensoi had the lowest shoot production of the four species. However data collected over one summer indicated a large proportion of energy may be directed into reproduction.

No data are available for A. forsteroides for the first summer but during both winters and the second summer A. forsteroides produced much more shoot dry matter at Mt. Field West than the other species. Its winter growth was particularly strong (indicating an extended growing season). However the response of this species on Mt. Wellington was similar to that of the other species. This is difficult to explain, given the similar responses from the Mt. Field sites covering some 330 m altitude, but may be related to severe nutrient stress resulting from more anaerobic soil conditions experienced on Mt. Wellington (table 2-3).

At Newdegate Pass where D. novae-zelandiae and A. forsteroides are growing in a complex mosaic, there is no evidence of A. forsteroides outcompeting or overgrowing D. novae-zelandiae. This observation and the variability of P. colensoi, D. novae-zelandiae and D. minimum between seasons and years suggest that net production is closely related to aspects of a highly variable climate and that dominance of growth of any one species is likely to be relatively short lived. Environmental and growth data would need to be collected over short intervals for several years to test this hypothesis.

Data from the soil analyses indicate that all sites are highly acidic and extremely nutrient poor, all sites show similar soil analyses which is not surprising given their close proximity and similar lithology. Under conditions of high acidity and poor aeration peat decomposition is very slow and nutrient availability extremely low (Swift et al. 1979, Sparling 1985, Vaughan and Ord 1985). The Kirkpatrick et al. (1985) hypothesis that cushion distribution is controlled in part by an east-west nutrient gradient cannot be fully tested by this study. It does appear that all species have a high tolerance to poor nutrient, low pH environments. Whether significant differences occur in soil nutrient conditions at the extremes of the species ranges remains to be tested.

From measurements of soil moisture it appears that P. colensoi and D. minimum occupy the best drained site, followed by D. novae-zelandiae then A. forsteroides on the most anaerobic. Water stress was completely absent during the two years of this study. These results agree reasonably well with both field observations (Kirkpatrick et al. 1985) and inferred gradients (Gibson and Kirkpatrick 1985b). However at Mt. Field P. colensoi and D. minimum occupy sites which rarely fall below field capacity in addition to well drained sites on steep rocky slopes implying wide environmental tolerances. The poor growth rates of A.

forsteroides at Mt. Wellington compared to Mt. Field may be correlated with the water logged nature of this site.

The above ground net production of cushion species in Tasmania (282-709 g/m^2/year) was found to be greater than that reported from New Zealand (119-414 g/m^2/year) which in turn was greater than that reported for physiognomically similar communities in the northern hemisphere (68-140 g/m^2/year) (Bliss 1956, 1966; Svoboda 1973; Bliss and Mark 1974). The higher net production achieved in New Zealand compared to the northern hemisphere has been attributed to a longer growing season and greater shoot densities per unit area (Bliss and Mark 1974). The alpine environments studied in this thesis have a longer growing season than New Zealand (in excess of six months) and a similar density of shoots. The differences in above ground primary production between Tasmania and New Zealand largely result from this extended growing season as well as higher temperatures (see figure 2-4 and Bliss and Mark 1974 -table 2).

The lack of significant seasonal snow lie, the thermal properties of the cushion form, the evergreen habit of the bolster in Tasmania and the variability of the climate suggest a potential growing season of 10-12 months. The exact length of the growing season in any year will depend upon the prevailing climatic conditions. Winter conditions would rarely be so mild as to allow the full realization of the growing season. Nonetheless significant periods of mild weather occur during most winters in which growth could occur. The growing season in Tasmania is likely therefore to be both intermittent and of variable length.

If a 365 day growing season is assumed for the Tasmanian data, this results in shoot productivity of 1.6-1.7 g/m^2/day compared with those of 0.8 g/m^2/day reported from New Zealand (Bliss and Mark 1974). Surprisingly the bolster species from Macquarie Island have similar productivities to Tasmania (0.9-2.0 g/m^2/day), despite a much colder environment (appendix 3). However it should be noted that the Macquarie Island data may be an overestimate since they are based on only a part of a growing season.

There are several other significant differences between the cushion species of Tasmania and New Zealand. Bliss and Mark (1974) report vertical growth of 3-8 mm/year compared with 0.7-2.3 mm/year found at Mt. Field. More recent

work from Central Otago suggest rates of 0.8 mm/year (Roxburgh et al. 1988). P. colensoi on Mt. Field has shoot densities 40% lower than those reported from Central Otago (Bliss and Mark 1974).

CHAPTER 3 LATERAL SPREAD AND SIZE CLASS ANALYSIS OF TWO CUSHION SPECIES FOLLOWING FIRE.

3.1 Introduction

Observation has shown that D. novae-zelandiae, A. forsteroides and P. lawrencii can recover rapidly from subsurface axial buds following fires hot enough to kill all live leaves. More severe fires can partially or completely consume entire cushions with subsequent vegetative recovery being generally poor. These three species can rapidly reinvade burnt areas provided a seed source is close by. Dracophyllum minimum is apparently much more susceptible even light fires and does not appear to readily reinvade burnt areas. The response of P. colensoi to fires is not known.

Following hot fires revegetation is normally very slow in the Tasmanian alpine zone with complete cover taking up to 40 years to re-establish (Kirkpatrick and Dickinson 1984). Under such conditions of low competition estimates of horizontal and vertical growth rates of cushion plants and population age distribution (estimated from size) can be obtained where fire events can be accurately dated.

Four such areas occur at Mt. Field and Mt. Wellington and are being reinvaded by A. forsteroides and a further area at Mt. Field is being reinvaded by P. lawrencii. This chapter reports the growth rates and size class distributions of the cushion species found in these areas.

3.2 Study areas

The alpine area at Mt. Field has been subject to two major fires in the last 25 years. The first fire occurred in 1962 and was restricted to the northern area of the park and burnt from Lakes Belton and Belcher up to the edge of the Mawson plateau . The second fire in 1967 was much more widespread resulting from numerous spot fires originating from an escaped regeneration burn in the Florentine Valley to the west. This fire burnt out extensive areas of the alpine communities of Mt. Field West and the Rodway Range.

Two plots were established on the Mawson plateau, one in the area burnt in 1962 in which A. forsteroides is re-establishing and the second in the adjacent

unburnt vegetation to allow comparison of size class distributions. Two more plots were established in areas of A.forsteroides regeneration near Clemes Tarn an area burnt in 1967. A further plot was located at Newdegate Pass in an area of P. lawrencii regeneration dating from the 1967 fire.

Both 1962 and 1967 were bad fire years in Tasmania with parts of the alpine area of Mt. Wellington burning in both years. In 1962 the fire was relatively small, being confined to the summit area. The 1967 fire was very severe and burnt out all of the Dead Island plain and most of the surrounding forest and a large part of Hobart. Two plots were located in each area where A. forsteroides regeneration was measured.

3.3 Methods

At each site 10 m x 10 m plots were laid out and the diameters of all cushion plants falling within these plots were measured. The diameter data were divided into 20 mm size classes, and histograms were produced for each plot. The number of cushions per plot ranged from 63 to 271. For 165 randomly selected individuals at the Dead Island site both diameter and height were measured. Height was determined with a vertical ruler and a level. The data were collected in the late 1982.

3.4 Results

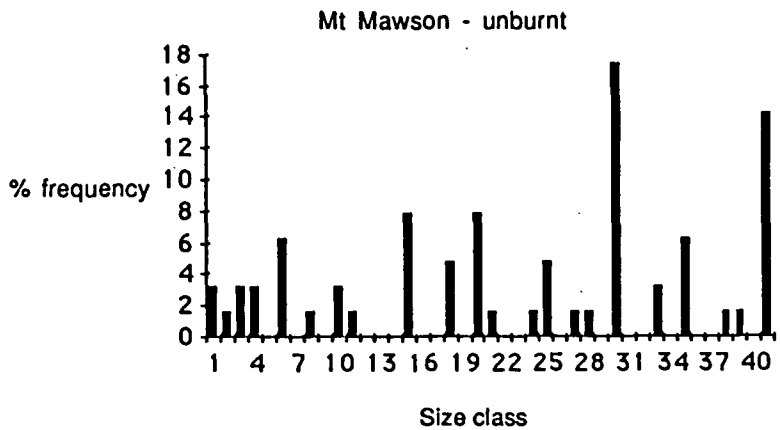
The size class distribution of A. forsteroides on the Mawson plateau in the unburnt plot is shown in figure 3-1(a). A second plot was laid out in the area burnt in 1962 immediately adjacent to plot 1 and its size class distribution is shown in figure 3-1(b).

In the unburnt plot size classes across the entire range (to >800 mm diameter) are represented, with only a small bias toward several of the larger size classes.The total number of individuals in this plot were 63. The adjacent burnt plot had similar aspect, slope, ~~or~~ drainage conditions. It seems reasonable to assume a uniform vegetation across the site prior to the fire. The size class distribution of cushions in this plot is radically different to the unburnt plot. Evident is the typical reverse J-shaped curve indicating continuous recruitment up to size class 11 (201-220 mm diameter) with only a few larger individuals being present, these presumably having survived the fire.

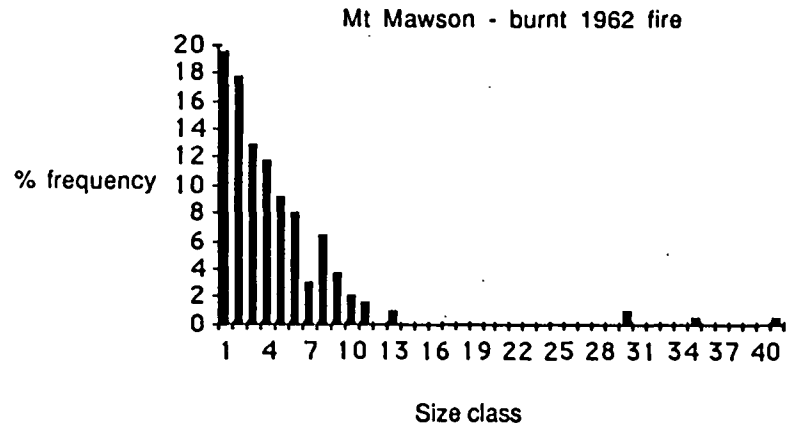
land?

Figure 3-1 Histograms of the frequency of size classes of diameters of A. forsteroides cushions. Size classes are in 20 mm intervals (a) plot 1 on Mt. Mawson, unburnt; n=63. (b) plot 2 on Mt. Mawson, burnt 1962; n=185. (c) plot 1 on Mt. Wellington burnt in 1962; n=132. (d) plot 2 on Mt. Wellington burnt in 1962; n=310.

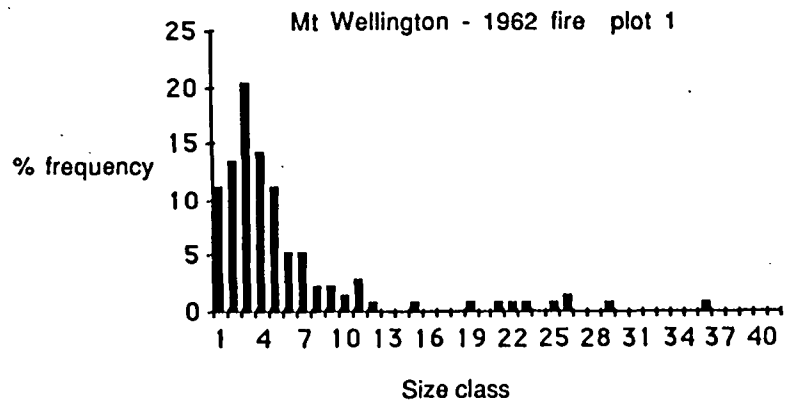
a


Mt Mawson - unburnt
% frequency
0 2 4 6 8 10 12 14 16 18
1 4 7 10 13 16 19 22 25 28 31 34 37 40
Size class

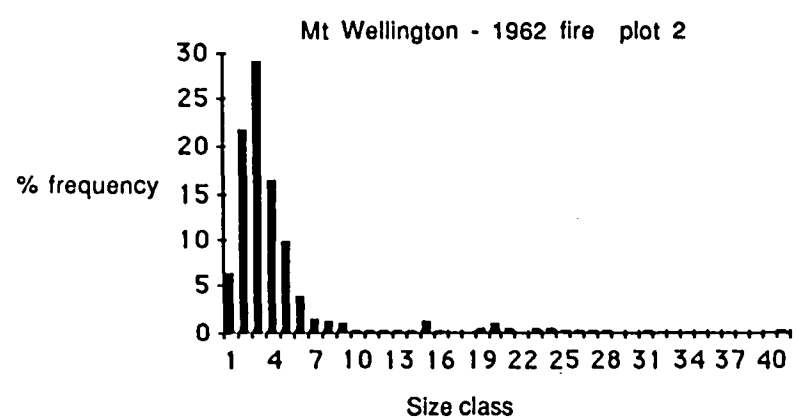
b


Mt Mawson - burnt 1962 fire
% frequency
0 2 4 6 8 10 12 14 16 18 20
1 4 7 10 13 16 19 22 25 28 31 34 37 40
Size class

c


Mt Wellington - 1962 fire plot 1
% frequency
0 5 10 15 20 25
1 4 7 10 13 16 19 22 25 28 31 34 37 40
Size class

d


Mt Wellington - 1962 fire plot 2
% frequency
0 5 10 15 20 25 30
1 4 7 10 13 16 19 22 25 28 31 34 37 40
Size class

The number of individuals in the plot is almost three times that of the unburnt control.

Size has generally been used as an indicator of age (this has been particularly true in studies on tree species Veblen and Stewart 1982, Read and Hill 1985, Cullen 1987 and others) although the difficulties of this relationship are well known (Harper 1977; Ogden 1985a, 1985b). To demonstrate the validity of the size - age correlation in cushion plants would require many years work as there appears no way of dating individual cushions (with the possible exception of D. minimum). Nonetheless it seems reasonable to assume such a relationship especially in the burnt areas where direct competition is low or absent (total cover for all burnt areas was estimated to range from 20-30%). Size was therefore assumed to be related to age and the relationship was assumed to be linear in the absence of other data.

Under this assumption the first group of seedlings to be recruited after the fire would be size class 11 (201-220 mm diameter). Given the 20 year gap between the 1962 fire and data collection (1982), this implies a lateral growth rate of 11.0 mm/year. The other sites show similar growth rates (table 3-1, figures 3-1 and 3-2). In all cases the size class of the first post fire recruitment was taken to be the last of the continuous classes or where the curves flattened out (figures 3-1 and 3-2). This assumption gave good correspondence between replicates.

Some plots showed a drop off in the smallest size classes, this may have resulted from either a drop off in germination in the last few years or alternatively a decrease in available germination sites.

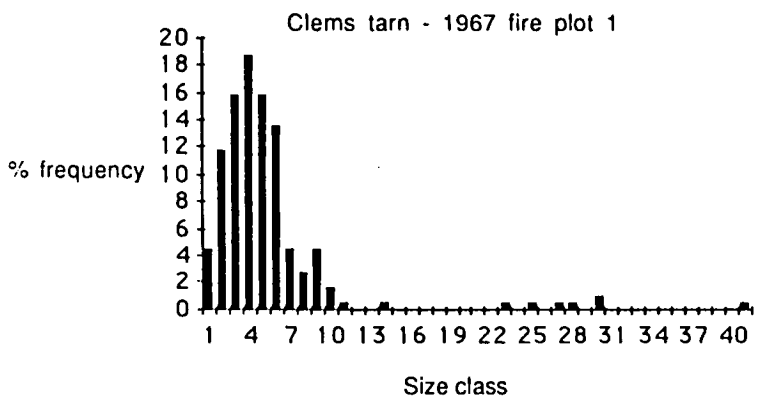
It is interesting to note that the sites at Dead Island had generally a slower lateral growth rate than the sites at Mt. Field, a result similar to that found in the growth study reported earlier.

The estimate for the lateral growth of P. lawrencii of 20.0 mm/year is somewhat greater than those calculated for A. forsteroides (6.7-14.7 mm/year, figure 3-3, table 3-1).

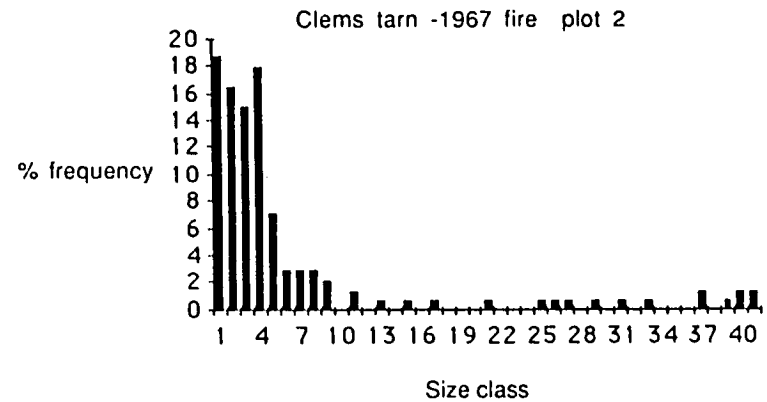
The relationship between height and diameter found for the A. forsteroides data from the Dead Island site is shown in figure 3-4. For cushions up to about 400

Figure 3-2 Histograms of the frequency of size classes of diameters of A. forsteroides cushions burnt in the 1967 fires. Size classes are in 20 mm intervals (a) plot 1 near Clems Tarn; n=176. (b) plot 2 near Clems Tarn; n=139. (c) plot 1 on Mt. Wellington; n=115. (d) plot 2 on Mt. Wellington; n=178.

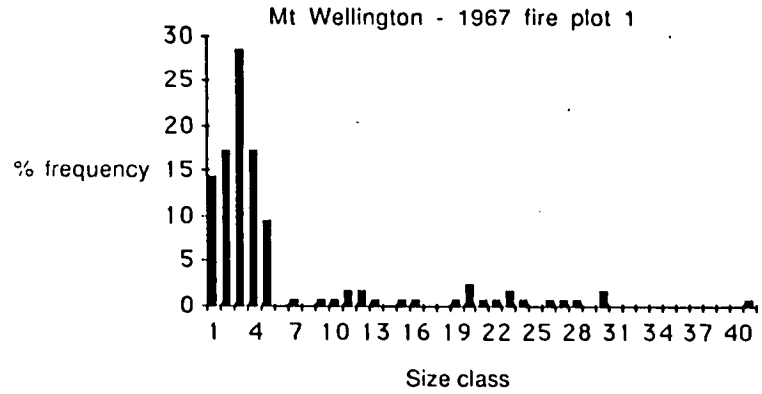
a


Clems tarn - 1967 fire plot 1
% frequency
0 2 4 6 8 10 12 14 16 18 20
1 4 7 10 13 16 19 22 25 28 31 34 37 40
Size class

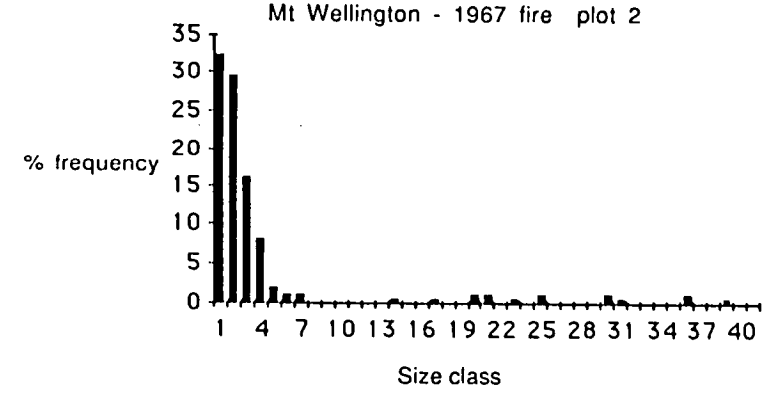
b


Clems tarn -1967 fire plot 2
% frequency
0 2 4 6 8 10 12 14 16 18 20
1 4 7 10 13 16 19 22 25 28 31 34 37 40
Size class

c


Mt Wellington - 1967 fire plot 1
% frequency
0 5 10 15 20 25 30
1 4 7 10 13 16 19 22 25 28 31 34 37 40
Size class

d


Mt Wellington - 1967 fire plot 2
% frequency
0 5 10 15 20 25 30 35
1 4 7 10 13 16 19 22 25 28 31 34 37 40
Size class

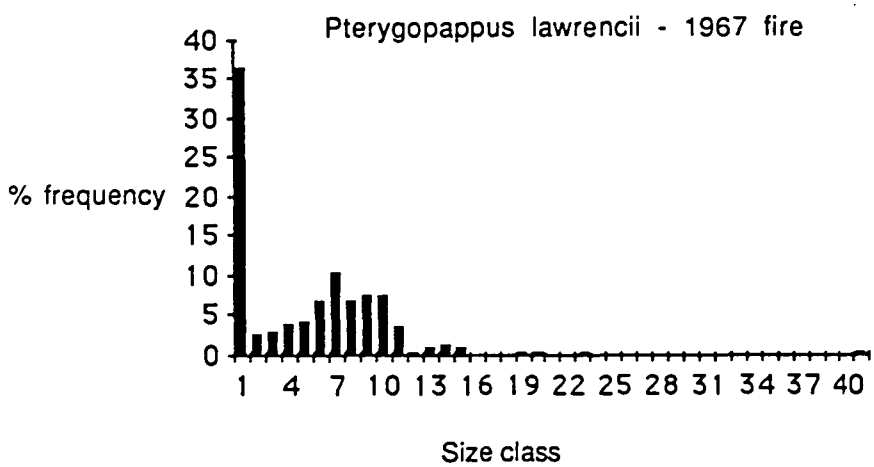


Figure 3-3 Histogram of the frequency of size classes of diameters of P. lawrencii cushions burnt in the 1967 fires at Newdegate Pass. Size classes are in 20 mm intervals; n=271.

Table 3-1 Lateral growth rates and cushion densities for two species of cushion plants growing in situations of low competition following fire.

	Fire year	Lateral growth rate (mm/year)	Cushion density (/100 m^2)
Abrotanella			
MT. FIELD			
Mawson -1 (1280 m)	-	-	63
-2	1962	11.0	185
Clemes tarn -1 (1200 m)	1967	14.7	176
-2		12.0	139
MT. WELLINGTON			
Summit -1 (1270 m)	1962	9.0	132
-2		12.0	310
Dead Island -1 (1150 m)	1967	6.7	115
-2		9.3	178
Pterygopappus			
MT. FIELD			
Newdegate Pass (1300 m)	1967	20.0	271

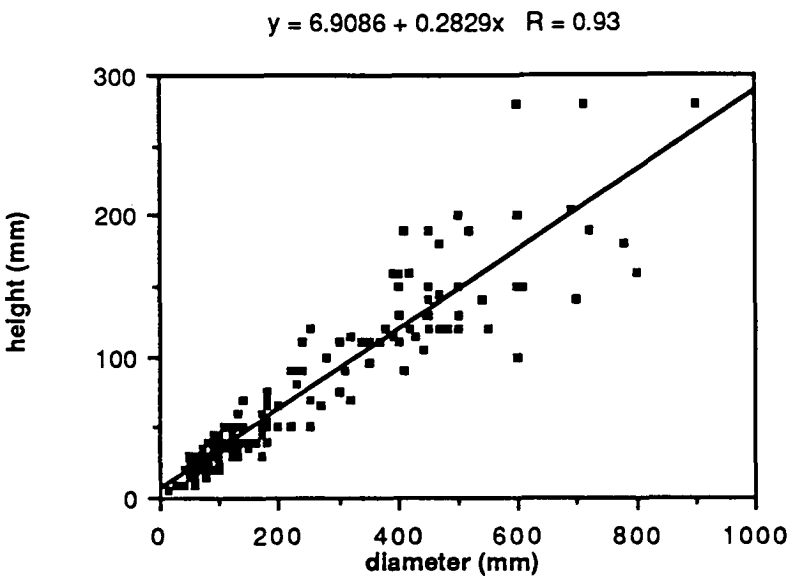


Figure 3-4 Plot of height against diameter for Abrotanella forsteroides from Mt. Wellington.

mm diameter there appears to be a good linear relationship between height and diameter. For larger cushions the regression still fits the data but the spread of points becomes much larger. This is interpreted as showing influence of competition (for space or resources) on these large cushions which survived the 1967 fire. Restriction for space may result in larger than expected height growth.

The size class of the first post fire recruitment can be used to obtain an estimate of the rate of vertical growth over the 15 year period 1967-82 using the regression. The size class of the first recruitment are 5 and 7 for plots 1 and 2 respectively (figure 3-2). This results in estimates of vertical growth of 2.3-3.1 mm/year over the 15 year period. This accords reasonably well with the figure of 1.0 mm/year from the growth achieved during 1982/83 (table 2-5) given that we know little of the annual variability in growth rates.

3.5 Discussion

It seems that, in the absence of competition and with a propagule source close by, rapid and sustained recruitment of A.forsteroides and P. lawrencii seedlings can occur on bared areas. If the assumption that size reflects age is correct then seedlings appear to be recruited continuously as evidenced by the occurrence of seedlings in all the smaller size classes. The data were tested against a negative exponential model for continuously regenerating populations with a constant mortality rate ($y = y_0 e^{-xb}$ where y is the number of cushions in age class x, y_0 is the initial population at time zero and b is the mortality rate - Hett and Loucks (1976)). All data gave highly significant fit to this model (table 3-2) although systematic errors in the residuals were generally present possibly indicating that better models could be developed. The dynamics of cushion plant populations will be dealt with in more detail in the second section of this thesis.

Lateral growth rates of A. forsteroides under conditions of low competition falls in the range 6.7-14.7 mm/year averaged over a 15-20 year time period. This is considerably faster than the 2.9 mm/year reported for D. novae-zelandiae at 895 m asl in New Zealand (Lough et al. 1987). The New Zealand data refer to a closed cushion vegetation so that competition effects may be restricting lateral spread of these cushions. Interspecific differences have not been determined and these may also contribute to the difference between the reported rates.

Table 3-2 Statistic on the goodness of fit of the cushion size class data to the negative exponential model of continuous regeneration with a constant mortality rate through time.

	Fire year	F ratio	Probability
Abrotanella			
MT. FIELD			
Mawson -1 (1280 m)	-	0.17	0.684
-2	1962	145.46	<0.001
Clemes tarn -1 (1200 m)	1967	76.26	<0.001
-2		70.24	<0.001
MT. WELLINGTON			
Summit -1 (1270 m)	1962	133.13	<0.001
-2		121.64	<0.001
Dead Island -1 (1150 m)	1967	42.10	<0.001
-2		57.26	<0.001
Pterygopappus			
MT. FIELD			
Newdegate Pass (1300 m)	1967	110.19	<0.001

CHAPTER 4 MODELLING CUSHION PLANT DISTRIBUTION PATTERNS

4.1 Introduction

All four cushion species have overlapping geographic ranges and occasionally all four species are found within a relatively small area. However, habitat differentiation has been noted in the literature (Gibson and Kirkpatrick 1985a, 1985b; Kirkpatrick et al. 1985). The aim of this chapter is to attempt the construction of a model that reflects the habitats of these four species. To this end, both a climate model and published data are used.

4.2 Methods

BIOCLIM is a climatic modelling program that uses species site location and altitude records to define twelve climatic variables (called a climate profile) from climate surfaces calculated from available meteorological data (Nix, Hutchinson and Busby, in Busby 1986). This climate profile is then matched against the predicted climate in 0.1° latitude/longitude grid squares across Tasmania. The predicted climate in each grid square is derived from a single 'average' point within the grid.

Busby (1986) used this model to define and predict Nothofagus cunninghamii distribution in Tasmania and South-eastern Australia. Gibson (1986) used the model on Lagarostrobos franklinii and found that while the climate profile made ecological sense, the predicted range of the species gave a poor fit. He suggested that this resulted from the predicted climate within each grid being too coarse for species with narrow climate profiles or for species occurrences in areas with steep local environmental gradients.

The model also has a problem with circularity. That is, it needs input data from the entire geographic and altitudinal range of species to generate the climate profile and then it uses this profile to predict the species range.

For each of the four cushion species, climate profiles and predicted distributions were generated using BIOCLIM. Input data for D. novae-zelandiae (56 sites), D. minimum (34 sites) and A. forsteroides (60 sites) covered their known geographical and altitudinal ranges. For the restricted P. colensoi 17 records from all 12 known locations were used.

4.3 Results and discussion

The climate profiles of the four bolster species are shown in figure 4-1 (means and 90% confidence limits). Altitudinal ranges of the four species are shown in figure 4-2 (after Kirkpatrick et al. 1985), and distribution patterns are shown in figure 4-3.

Kirkpatrick et al. (1985) noted overlapping altitudinal ranges in the four species and indirect gradient analysis suggested that altitude (or its environmental correlates) to be one of the important gradients determining distribution patterns. However the 700 m variation in altitude of the climatic treeline and its frequent absence made it difficult to interpret precisely what altitude is measuring. On any one mountain P. colensoi and D. minimum tend to occur at the highest elevations above the climatic treeline. Donatia novae-zelandiae and A. forsteroides often occur in these same communities but can extend well below the treeline in boggy or wet subalpine areas which are occasionally burnt.

The first six elements of the climate profile relate to temperature and all four species show similar orderings to altitude of these parameters (figures 4-1, 4-2). Correlations of temperature decline with increasing altitude are well known. It is interesting to note that for all parameters there is considerable overlap between all four species.

Phyllachne colensoi occupies the coldest habitat (lowest mean annual temperature, mean minimum of coldest month, mean maximum of hottest month, mean temperature of wettest quarter, mean temperature of the driest quarter). D. novae-zelandiae occupies the warmest habitats but it differs little from A. forsteroides All species have a very similar temperature range (and variance) of approximately 17.5° C. Given the difference in mean annual temperature preference this results in the regular overall upward displacement of species noted by Kirkpatrick et al. (1985). This displacement is never total given the large overlap in temperature preferences (figure 4-1) and microclimatic differences at any particular altitude as a result of variation in slope and aspect.

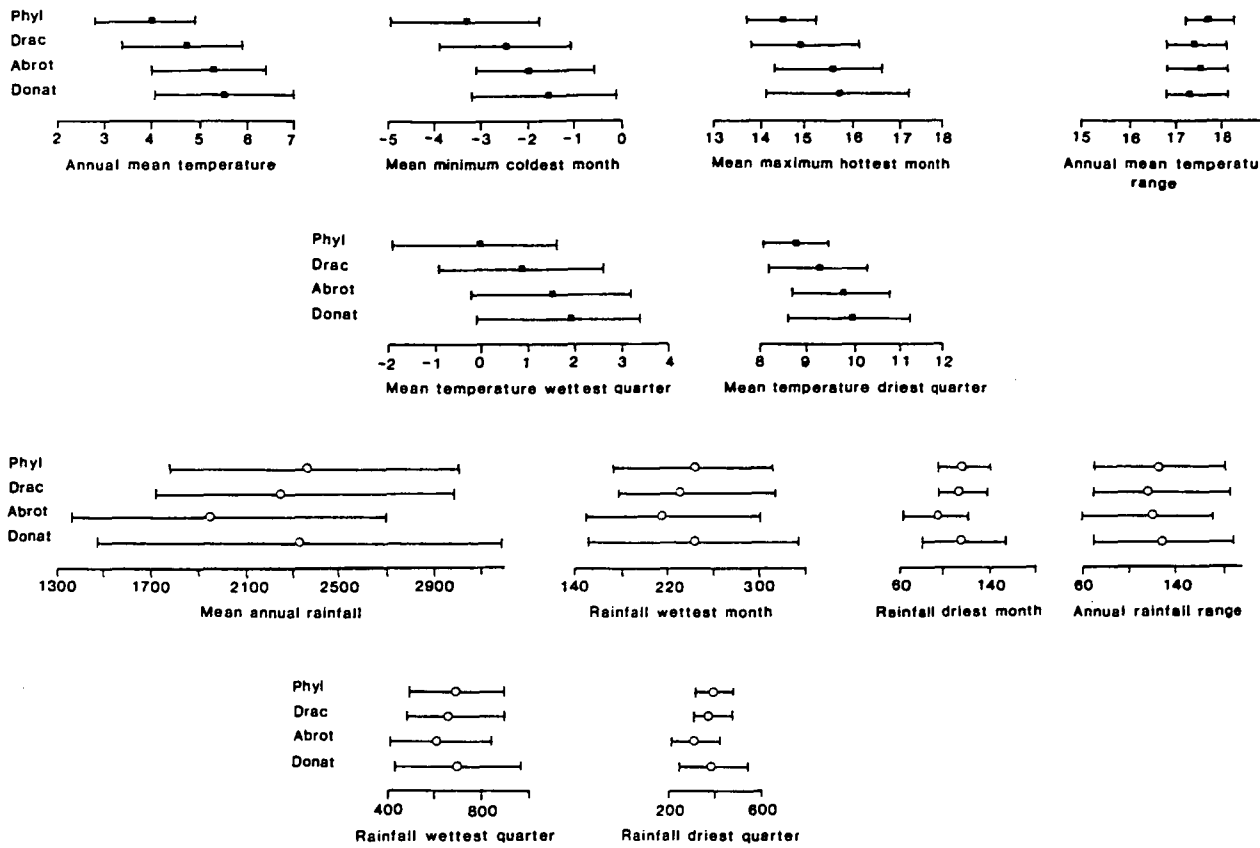


Figure 4-1 Climate profile for each of four bolster species. For each parameter of the profile the mean value and the 90% confidence limits are shown. (Temperatures in °C, rainfall in mm.)

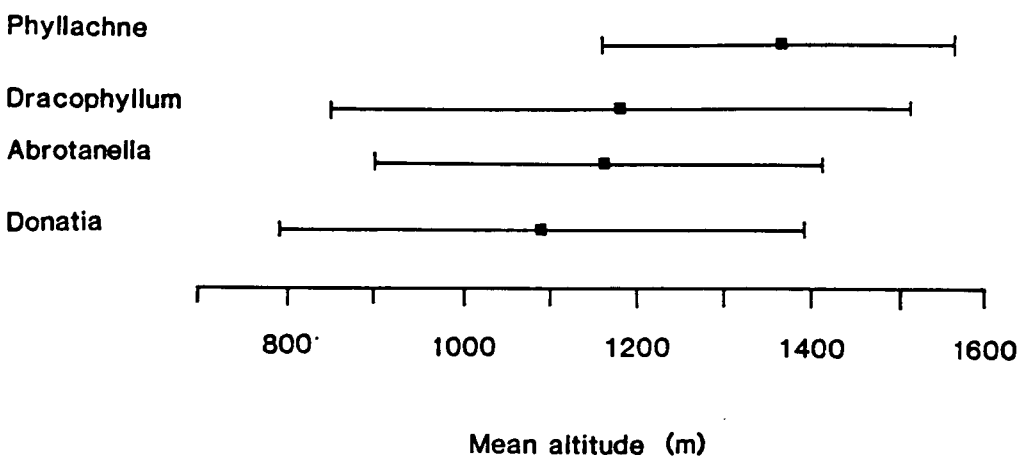
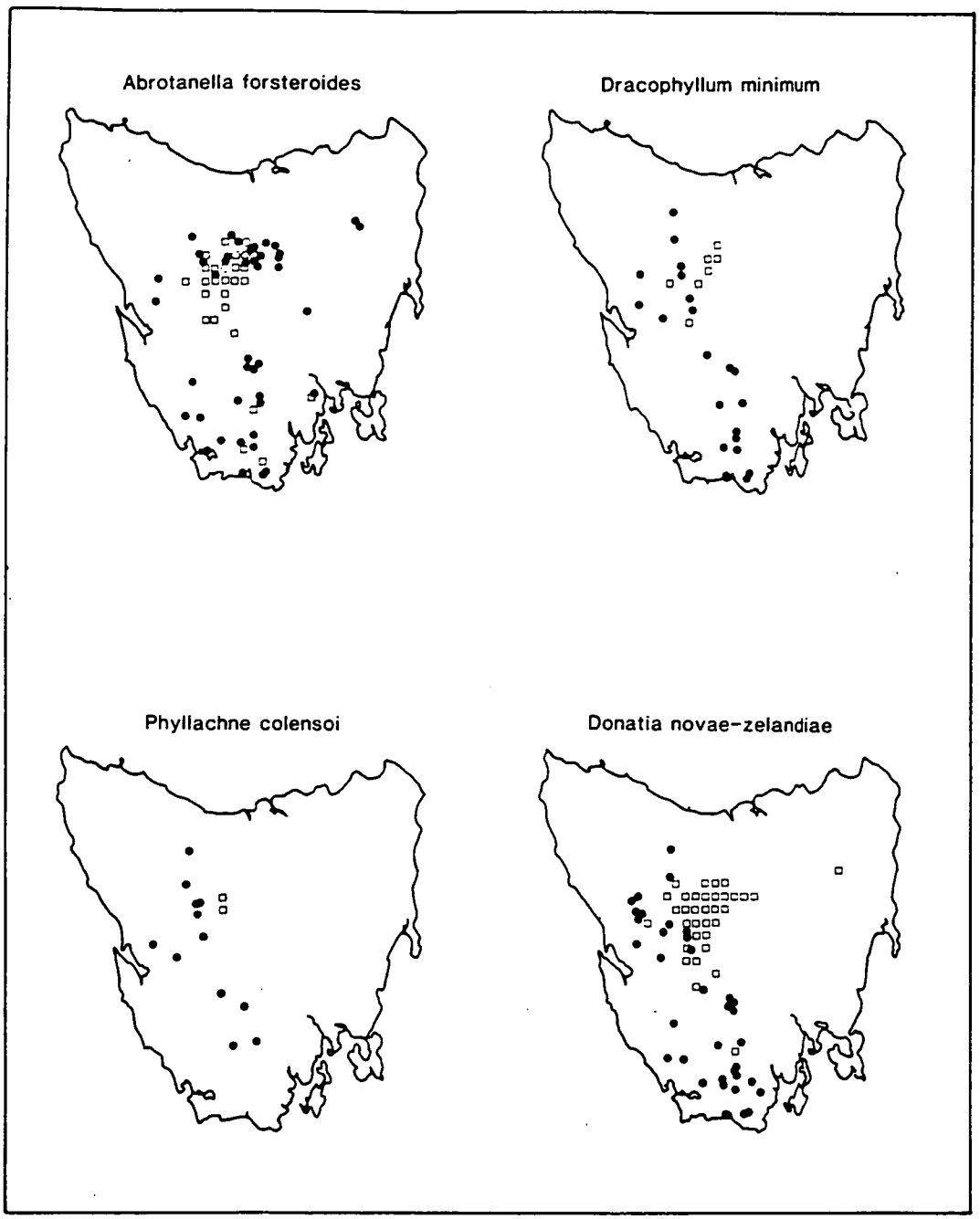


Figure 4-2 Mean altitude and 95% confidence intervals for each of the four bolster species (data derived from Kirkpatrick et al. 1985).

Figure 4-3 Predicted distribution patterns of the four bolster species. Solid circles represent input data (some represent more than one record). Open circles represent grid cells with a suitable climate, open squares represent grid cells with a marginal climate. (Note: BIOCLIM uses 0.1° grid not the 10 km square grid.)



The six climate profile parameters relating to rainfall are of less use in defining the particular species habitat preference. This stems from two reasons. Firstly all species occur in areas of high rainfall (mean annual rainfall 1950-2375 mm) with mean rainfall in the driest month in excess of 90 mm (figure 4-1). This implies that soil moisture would rarely be limiting. Secondly D. novae-zelandiae and A. forsteroides in particular are considered bog species (Jackson 1981, Kirkpatrick 1983, Gibson and Kirkpatrick 1985a, Kirkpatrick et al. 1985) and thus occupy sites with high soil moisture under a variety of rainfall conditions. A. forsteroides has the northeastern most distribution of the four species (figure 1-1) and as a consequence of rainfall pattern (see figure 8 in Gibson and Kirkpatrick 1985a) extends into the driest environments. However, within these environments it is preferentially found in low lying drainage lines. Thus rainfall is of little use in predicting species distributions.

Distribution patterns were predicted by BIOCLIM by matching climate profiles with estimated climate within grid cells. If ten or more of the estimated climate parameters for a grid cell fell within the interquartile range (i.e. between the 25 and 75 percentiles) of the climate profile of a species, and the remaining climate parameters fell within the total range of the climate profile, then that grid square was considered to possess a suitable climate for that species. Similarly, if all twelve climate parameters for a grid cell fell within the total range of the climate profile for a species, then that cell was considered to possess a marginal climate for that species.

The predicted distributions of the four species based on their climate profiles are poor fits compared with actual distribution patterns (figure 1-1 cf. 4-3). As with Huon pine (Lagarostrobos franklinii) this is likely to be the result of a poor estimate of the actual climate (based on one point) in each grid square (Gibson 1986). An alternate hypothesis is that the climate profiles are a poor estimate of the species requirements. This is rejected since the profiles obtained for the four cushion species and that of Huon pine make good ecological sense and agree with perceived responses to environmental gradients. Also, the non prediction of grid cells in which input data occur, suggests that the grid cell climate estimates are inaccurate. Nevertheless the predicted distributions have several interesting features.

A suitable climate was predicted to exist for A. forsteroides in only four grid cells. No other grid cell had a suitable climate for any of the other three species. Indeed the marginal habitat predicted for D. novae-zelandiae, A. forsteroides, and D. minimum largely fell within known ranges of these species but badly underpredicted them. For both D. minimum and D. novae-zelandiae marginal habitat was also predicted in the Central Plateau, an area in which only A. forsteroides currently occurs. If it is accepted that suitable habitat does exists for D. novae-zelandiae and D. minimum on the Central Plateau (based on the BIOCLIM predictions), then their absence may be explained in terms of past climatic history. It is possible that D. novae-zelandiae and D. minimum were eliminated from eastern Tasmania during the height of the Last Glacial and these species may still be re-occupying their potential range from a western source. It is interesting to note that marginal habitat exists for D. novae-zelandiae in a single cell at Ben Lomond, a highland area in north-eastern Tasmania.

Two occurrences of marginal habitat are also predicted for P. colensoi on the western Central Plateau. These areas are botanically well known and it is unlikely that P. colensoi occurs there.

From the climate profiles generated by BIOCLIM a model of species responses to temperature can be inferred (figure 4-4). Data from New Zealand confirms distribution patterns of P. colensoi and D. novae-zelandiae in relation to altitude (Gibson and Kirkpatrick 1985a).

In addition to the environmental correlate with altitude, soil aeration, soil nutrients and recovery after fire have been proposed as delimiting the distribution for the cushion plant species (Chapter 2, Martin 1940, Jackson 1973, 1981, Kirkpatrick 1982, 1983, Gibson and Kirkpatrick 1985b, Kirkpatrick and Dickinson 1984, Kirkpatrick et al. 1985).

While physical drought is rarely experienced by any species (table 2-3) and all species have broad tolerances to high soil moistures, A. forsteroides tolerates the most anaerobic conditions. Table 2-3 shows that soil moisture of the A. forsteroides sites on Mt. Field West, Wombat Moor and Mt. Wellington were above saturation (58-71% of sampling times over 24 months) for longer than the other bolster species. D. novae-zelandiae showed the next highest tolerance to saturated soil conditions (42-50%, Broad Valley and Mt. Field

West) followed by P. colensoi and D. minimum (29% and 21%, Mt. Field West) which showed essentially similar tolerances.

These conclusions agree with those inferred by Gibson and Kirkpatrick (1985b) and Kirkpatrick et al. (1985) from indirect gradient analysis. Major differences between P. colensoi and D. novae-zelandiae are also recorded from New Zealand where D. novae-zelandiae is more or less restricted to the subalpine bogs while P. colensoi which also occurs in subalpine bogs is by no means restricted to them. It also occurs in the most exposed sites as well as in areas of the longest snow lie in the high alpine zone (Burrows 1977a, 1977b; Gibson and Kirkpatrick 1985a). The presumed habitat preferences of cushions in relation to soil aeration are shown in figure 4-5).

Not so! (see Bliss+Fah '80

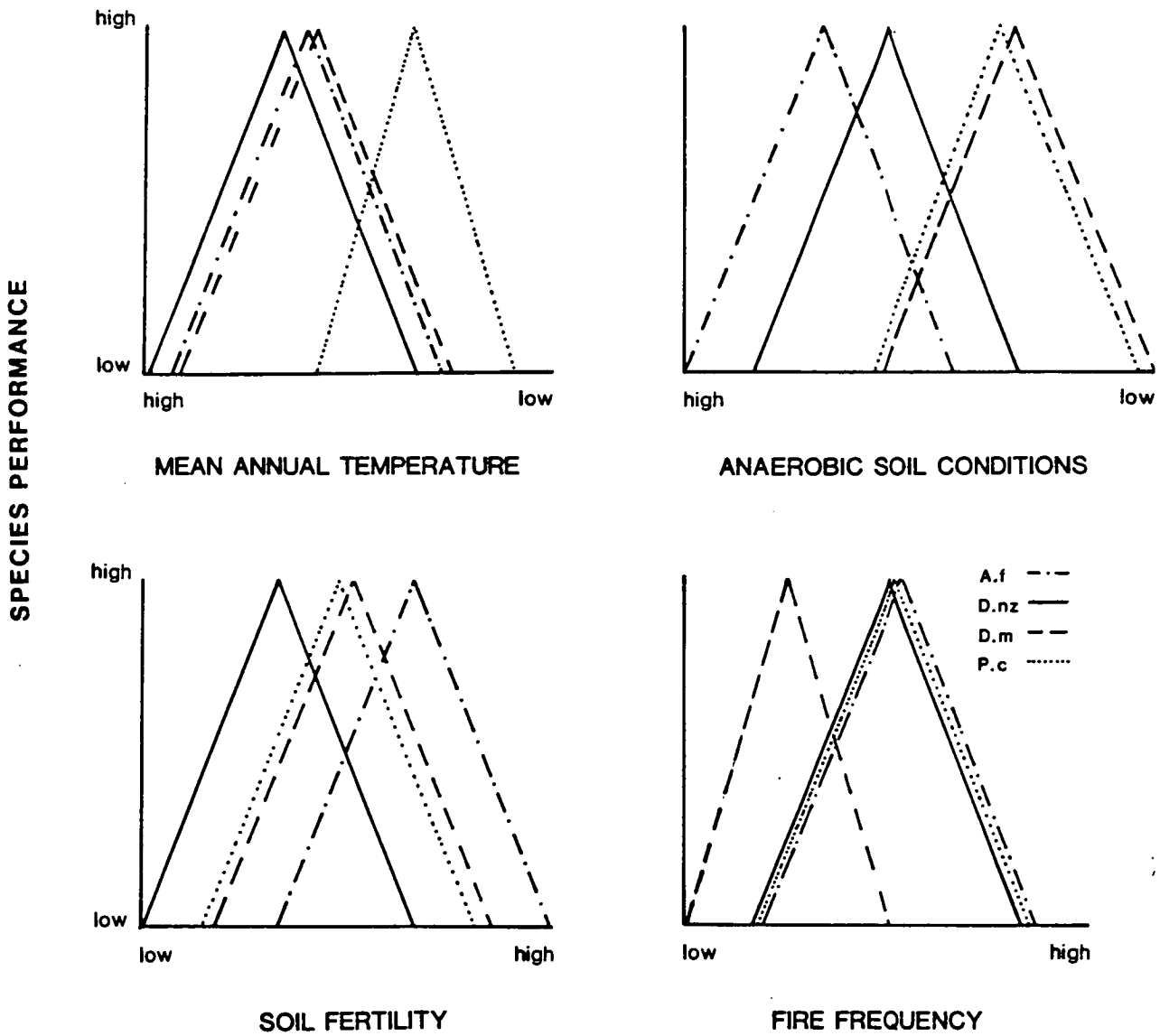
The high tolerance of A. forsteroides to anaerobic conditions may be related in part to anatomical differences (Chapter 9). A. forsteroides leaves and stems contain large ducts which may have a role in oxygen transport.

Kirkpatrick (1982) and Kirkpatrick et al. (1985) have hypothesized that the SW-NE floristic gradient across Tasmania shown by analysis of alpine and bolster data, is related to a precipitation and soil fertility gradient. There is no direct evidence of differential nutrient preference between cushion species. The magnitude of nutrient differences between the peats of western and eastern mountains in bog situations of low pH and poor drainage may be minimal given the low amounts of available nutrients generally available under these conditions (Swift at al. 1979, Sparling 1985). The inferred soil fertility preference of the cushion species is shown in figure 4-4 (Kirkpatrick et al. 1985).

During recent time the Tasmanian alpine areas have been subject to increased fire frequency with 16% being burnt between 1960-80 (Brown et al. 1983b). These fires have allowed observations to be made on the response of cushion species to fire. Kirkpatrick (1983) suggests that at low elevation in eastern Tasmania A. forsteroides bolster heath is dependent on fire for its perpetuation, otherwise being overgrown by graminoids and shrubs. The same may be true of low elevation occurrences of D. novae-zelandiae in western Tasmania.

At higher elevations on Mt. Wellington (burnt 1967), Mt. Field (burnt 1967) and Central Plateau (burnt 1983), A. forsteroides shows strong vegetative

Figure 4-4 Inferred performance of the four bolster species in relation to temperature, anaerobic soil conditions, soil fertility and fire frequency.



recovery from axillary buds where the bolsters were not consumed. In addition seedling production is often high. The same observations apply to D. novae-zelandiae at Mt. Field. D. minimum however, appears sensitive to fire and is often killed outright even when the cushion is only scorched. The response of P. colensoi to fire is less easy to quantify because of the few sites at which it occurs. The dominant area of P. colensoi at Mt. Field West appears to be associated with an old (pre-1967) fire scar, so it is assumed to have a similar response to D. novae-zelandiae and A. forsteroides. The responses of these species to fire are illustrated in figure 4-4.

Alpine species are generally considered to have large environmental tolerances because of low intraspecific and interspecific competitiveness (measured by growth rates) (Grime 1979, Noble 1981). The shape of curves in figure 4-4 therefore could well involve a wide plateau, at optimal species performance values. In addition there may be significant interaction between factors given that species niches are determined by multivariate interactions not simplistic univariate responses.

Given these limitations, the model of species responses to environmental factors shown in figure 4-4 can largely explain the species distribution patterns found in Tasmania. Of these factors temperature and tolerance to anaerobic conditions are likely to be of major importance. The suggested niche of the four species as defined by these two factors is shown in figure 4-5. Altitude and/or drainage have been suggested to be major gradients determining vegetation patterns in Tasmania in a number of local and regional studies (Minchin 1983; Kirkpatrick 1983; Kirkpatrick et al. 1985; Gibson and Kirkpatrick 1985a, 1985b; Kirkpatrick 1984).

This model largely fits the distribution patterns of bolster species found in Tasmania. The blank area on the model corresponding to bogs at high altitude (in the top right of the figure) largely reflects a lack of these habitats rather than an absence of bolster species from them. The prediction of pure stands of D. minimum on well drained sites at low altitude overestimates that actually found. This may result from the replacement of D. minimum from these sites by tall shrubs and graminoids. The importance and quantification of species performance to these two factors needs to be defined by further field work and glasshouse competition experiments.

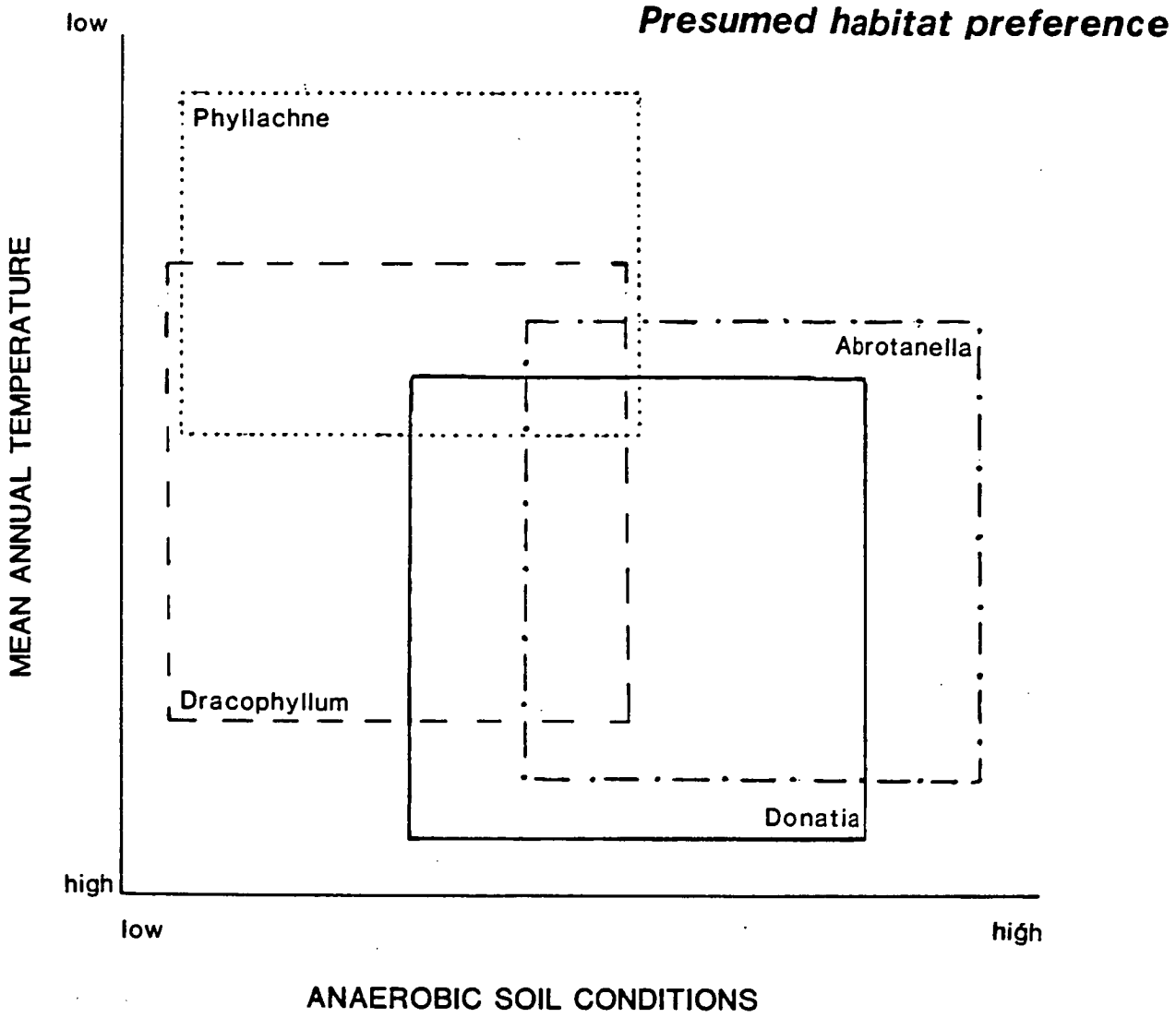


Figure 4-5 Presumed habitat preference of the four bolster species.

Past climatic history may also be of importance in the understanding of the cushion species distribution patterns. The results of the climate model simulations suggest that D. novae-zelandiae and D. minimum may still be expanding into their potential range over the Central Plateau. Likewise the presence of D. novae-zelandiae and absence of A. forsteroides from some of the mountains of south-eastern Tasmania (figure 4-3) may be the result of localized species extinctions during the Last Glacial and differential dispersal rates since it ended approximately 14,000 year b.p. Given the paucity of macrofossil evidence from Quaternary sites and the poor preservation of bolster species pollen (Macphail 1979, 1986; Gibson et al. 1987), the importance of historical events in the determination of extant bolster distribution patterns is likely to remain in the realms of conjecture.

CHAPTER 5 DYNAMICS AND SUCCESSION IN BOLSTER HEATH COMMUNITIES

5.1 Introduction

The second part of this thesis (Chapters 5-7) will address the mechanisms of succession and community stability in mosaic cushion plant communities. Data from the growth studies (Chapter 2) and pattern of reinvasion of bare areas by bolster species following fire (Chapter 3) generate several hypothesis relating to successional process and community stability. The data from the growth studies indicate that the competitive rankings (measured as dry matter production) between species are variable from season to season and year to year. This implies that the apparent stable community structure observed may not result from an equilibrium between cushion species competition and the environment. Further the data from the post fire recovery study indicates the potential for continuous regeneration under non limiting resource conditions (i.e space and perhaps nutrients) however the fine scale dynamics of the cushion mosaics (i.e. closed communities presumably under limiting resource conditions) are not known. These questions will be addressed by this section of the thesis.

Much work has been undertaken in an attempt to understand patterns of plant succession and species diversity in different plant communities (Diamond and Case 1986 and others). Two major theoretical frame works have been developed, these are generally referred to as the equilibrium and non-equilibrium theories of community structure.

Under the equilibrium theory all plant communities develop toward stable climaxes in equilibrium with the prevailing environment. Under this theory all changes result from the competitive exclusion principal and species co-existence is dependent on resource use differentiation. There are several modifications of this theory. If predators are introduced into the system then resource use differentiation can be relaxed with continued species co-existence. Alternatively species co-existence when competing for a single resource may occur in environments characterized by a large number of small patches of varying resource level (Cheeson 1986, Cheeson and Case 1986).

The sequence of vegetation succession under the equilibrium theory has generally been called the relay floristics model (Egler 1954) where pioneering

species initially invade a disturbed area and are subsequently followed by a series of more diverse and more highly competitive plant assemblages each capable of finer division of the available resources. This succession results in a highly efficient and stable climax community. Implicit in this model is the assumption that each seral community modifies the environment in such a way as to make it more suitable for the later successional species (Clements 1936, Loucks 1970, Connell and Slatyer 1977, Cheeson and Case 1986).

However equilibrium theory fails to explain all observed patterns of plant succession and species diversity (Grime 1979). As a result a second series of models have evolved generally called non-equilibrium models. These models have generally involved external processes in the maintenance of community stability and species diversity rather than competitive exclusion. They can be summarized under the following headings; (a) fluctuating environment with continuous or discontinuous competition; (b) changing climatic means; (c) slow competitive or random displacement (Cheeson and Case 1986).

Where environments are highly variable or where disturbance is sufficiently frequent (less than the life span of the dominant species) stable communities of high species diversity can exist without any of the limitations imposed under equilibrium theory (Loucks 1970, Grime 1979, Huston 1979). Under such conditions competition does not proceed to the stage where limited resources determine community composition (Drury and Nisbet 1971, Huston 1979). Instead community composition may be more a reflection of life history traits (e.g. lifeform, dispersal ability etc.) (Connell and Slatyer 1977, Cheeson and Case 1986).

Davis (1986) argues that there is no such thing as stable communities since the climatic means are continually changing. Thus all communities lag behind the climatic conditions under which they form. In the case of tree species this may be of the order of hundreds of years. Her arguments highlight the problems of temporal and spatial scale in discussions of vegetation dynamics. Ecologists generally consider stability in terms of perceivable change within their life span. While this may be reasonable for communities of short lived species it becomes less justifiable for forest communities where the dominant species often have life spans very much longer than that of the human observer.

Hubbell and Foster (1983) pursue a similar line of argument. They suggest that tropical forest tree species have identical or almost identical resource requirements. Therefore the population density of any species at any one time is largely a matter of chance. However, if an area is sufficiently large, rates of species elimination are relatively slow so apparently stable communities are found.

It is in this theoretical setting that the mechanisms of plant succession of mosaic bolster communities are examined. These communities have high species diversity (c. 30 species/m^2) and have been little studied (Martin 1940, Jackson 1973, 1981, Kirkpatrick and Dickinson 1984, Kirkpatrick and Gibson 1984). In contrast succession and successional processes have received some attention in the alpine and tundra areas of the northern hemisphere and New Zealand (e.g. Billings and Mooney 1968, Douglas and Ballard 1971, Bliss and Wein 1972, Wein and Bliss 1973, del Moral 1983, Lough et al. 1987, Roxburgh et al. 1988).

Jackson (1973, 1981) considered coniferous heaths to be the climax vegetation on protected high altitude, high rainfall sites in western Tasmania. Martin (1940) and later Jackson (1973) noted that bolster plants were able to block and change direction of minor drainage lines thus forming small pools or tarns. These authors produced a model where the change in drainage would eventually lead to the senescence of the bolster and its invasion by heath and shrub species, finally leading to the coniferous heath climax. Jackson (1981) later suggested that this succession may be cyclical. His model has never been tested.

The work reported in this chapter:
(a) tests the validity of the Martin and Jackson model of bolster community succession in mosaic bolster heath.
(b) determines the pattern of succession of bolster communities -
    (i) as it is presently occurring and
    (ii) historically from analysis of macrofossils.

The study site was located in an area of mosaic bolster heath - string bog at Newdegate Pass. This area is approximately 5 ha in extent and comprises a mosaic of coniferous heath, mosaic bolster heath, lichen covered dolerite boulders and numerous tarns, approximately 10% of which have drained and are in the process of revegetation. It is thus an ideal area to test models of

succession. The data collected on the dynamics of string bog formation and decay used to test Jackson's (1973) successional model was carried out in conjunction with J.B. Kirkpatrick and has been previously published (Kirkpatrick and Gibson 1984, see Appendix 1).

To determine the patterns of bolster succession a study of revegetation of drained tarn floors and examination of macrofossils in a peat core through a large cushion dam was undertaken.

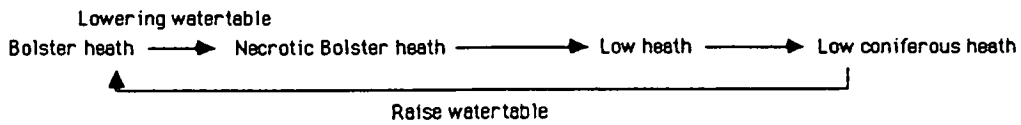
5.2 Dynamics of a string bog.

The Kirkpatrick and Gibson (1984) model partly supports that of Martin (1940) and Jackson (1973, 1981) and details the mechanism whereby tarn drainage and bolster necrosis occurs. However there are several important differences. Firstly the succession through low heath to low coniferous heath is only one possible pathway of community development. Secondly seedling recruitment of non bolster shrub species appears to be less important than the release from suppression of shrubs already present in the bolster heath. Kirkpatrick and Dickinson (1984), studying the recovery of alpine vegetation following fire, similarly concluded that such recovery was slow and that recruitment of conifer species from seedlings was very slow even after re-establishment of complete vegetation cover (40-50 years).

Figure 5-1 shows community relationships implicit in the Kirkpatrick and Gibson model. Which pathway is followed appears dependent on a variety of abiotic and biotic factors. The most significant abiotic factor is water table change (both lower and higher) while frost heaving effects may also be important. Biotic factors such as soil seed stores, dispersal rates, germination requirements and growth rates are probably also important.

A necrotic bolster heath (caused by a lowering of the water table) may proceed via low heath to a low coniferous heath as suggested by Jackson (1973). If, prior to changes in water table, the bolster heath contains conifers as a minor component, lowering the water table may lead directly to a low coniferous heath. If shrub seedlings are absent necrotic tarn walls can be re-invaded by cushion species, thus perpetuating the bolster heath on these sites. Changes in tarn wall location down slope may result in flooding of bolster or heath communities and their subsequent death. Alternatively a rise in water table, short of free surface

(a) Martin and Jackson model



(b) Kirkpatrick and Gibson model

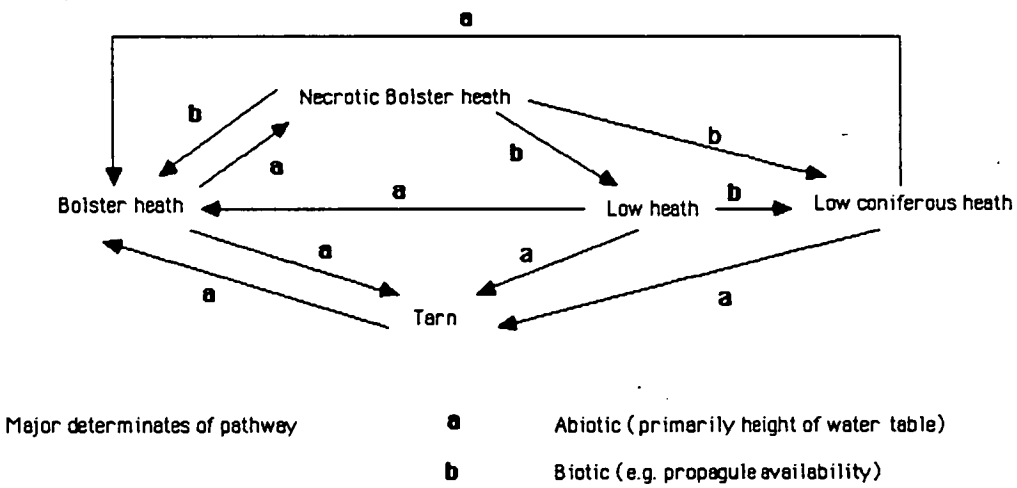


Figure 5-1 Two models of community succession in bolster heath communities, (a) Martin and Jackson's model, (b) Kirkpatrick and Gibson's model.

water, may result in low heath or coniferous heath reverting to bolster heath through enhanced bolster growth slowly subsuming the taller heath species (figure 5-1).

Jackson (1973) implied that the low coniferous heaths are the climatic climax vegetation of areas such as Newdegate Pass. However the work reported by Kirkpatrick and Gibson (1984) suggests that the long term trend is for upward expansion of the bolster heath encroaching and overwhelming the presently well drained coniferous heath abutting the exposed boulder fields. These bolster communities may undergo cyclical reversions to coniferous heath then back to bolster heath, after local changes in the water table due to tarn drainage. Similar cyclic changes have been suggested for cushion and turf communities in New Zealand (Lough et al. 1987).

Given the cyclical nature of these communities and the apparent stability through time at least in this location, it is more realistic to consider both these communities as part of a climax association (at least in the mid term -1000s years).

5.3 Species succession and persistence in bolster heaths.

The model of pathways of community development shown in figure 5-1, was partially tested by collecting data on species re-invasion of drained tarn floors. These provided bare surfaces of organic mud and/or rock surrounded by bolster heath. Succession through time was also studied by cuticular analysis of a core approximately 1 m in length taken from a bolster dam.

5.3.1 Methods

5.3.1.1 Vegetation analysis

Thirty-seven drained tarns of varying ages were located within the study area. Forty-nine quadrats were located in these tarns. Quadrat size was normally 5 m x 5 m though occasionally 2.5 m x 10 m quadrats were used due to tarn shape. This area is greater than the minimal area required for sampling this vegetation type (Kirkpatrick and Dickinson 1984). In each quadrat presence/absence data were collected for all vascular plants. Cover of vegetation, bare mud and rock were estimated to the nearest 10%.

The data set was classified using the polythetic divisive classification, TWINSPAN, which produces simple dichotomies (Hill 1979). The classification was stopped at the three group level.

5.3.1.2 Core analysis

Two cores were collected, using simple peat corers, from a cushion dam of 1030 mm depth. Core 1 was 50 mm in diameter. It compressed to a length of 525 mm on extraction. The core was subsequently cut in half lengthways and one half used for cuticular analysis. The amorphous peat of the core was cut into contiguous 5 mm sections and cuticle extracted initially by soaking samples in dilute hydrogen peroxide, then clearing in nitric acid and potassium chlorate. Colloidal organic matter was removed with 10% potassium hydroxide. The cuticle was then washed, stained and mounted.

This procedure resulted in degradation of some cuticle. To overcome this problem later samples were prepared by soaking in 10% chromic acid solution for 48 hours, then washing, staining and mounting. No pitting of cuticle was apparent using this technique.

Cuticle from the five major extant bolster species was similarly prepared and used as a reference (figures 5-2, 9-3, 9-5).

In most samples at least 250 cuticle fragments were identified and counted. The two Compositae species (A. forsteroides and P. lawrencii) had very similar cell wall detail but distinct leaf tip morphology, stomatal and trichome arrangements so counting was continued until 100 fragments of these two species were positively identified. Fifteen percent of samples produced less than 250 cuticle fragments and in those cases the entire sample was counted.

The top 90 mm of the core consisted of structured peat. This was divided into 10 mm layers and dominance assigned on a species dry weight basis.

A second core was taken alongside core 1 with a 100 mm diameter corer. A basal sample, 10 mm in height from this core was used for radio-carbon dating. This sample was gently sieved through 60, 599, and 1405 µm sieves. Approximately 0.15 g of wood was recovered and this material and the fine organic fraction (60-599 µm) was used for dating. Examination of the fine material under a

Figure 5-2

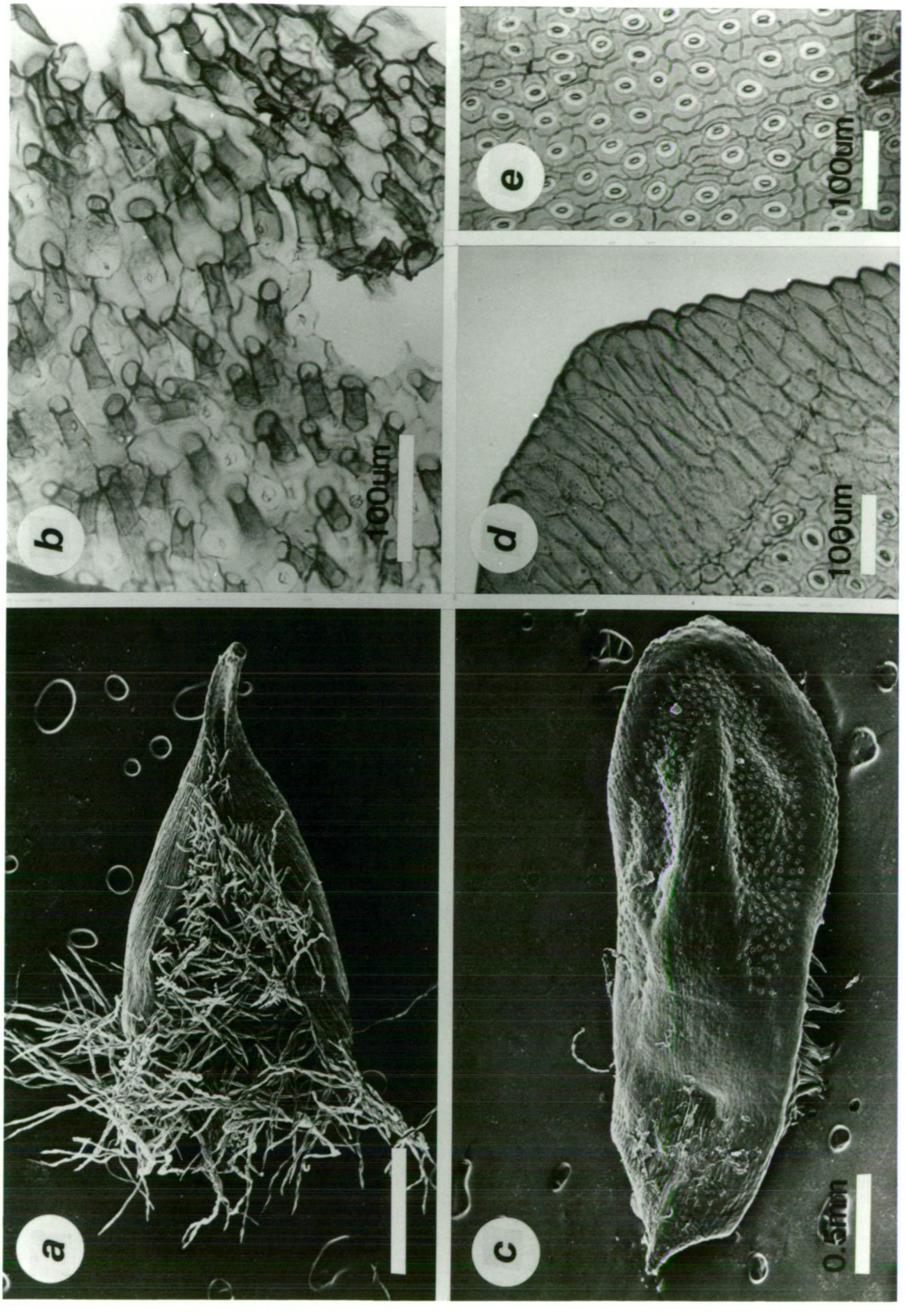
(a) Abaxial surface of Pterygopappus lawrencii clearly showing dense trichomes.

(b) Photomicrograph of trichome bases of P. lawrencii.

(c) Adaxial surface of Mitrasacme archeri.

(d) Photomicrograph of leaf tip of M. archeri.

(e) Photomicrograph of stomata arrangement of M. archeri.


a
b
100um
c
0.5mm
d
100um
e
100um

binocular microscope revealed numerous fine root hairs. This material might represent in situ roots or be of very much younger origin. Radio-carbon analysis was undertaken by the N.W.G. Macintosh Centre for Quaternary Dating, University of Sydney.

5.3.2 Results and Discussion

5.3.2.1 Vegetation analysis

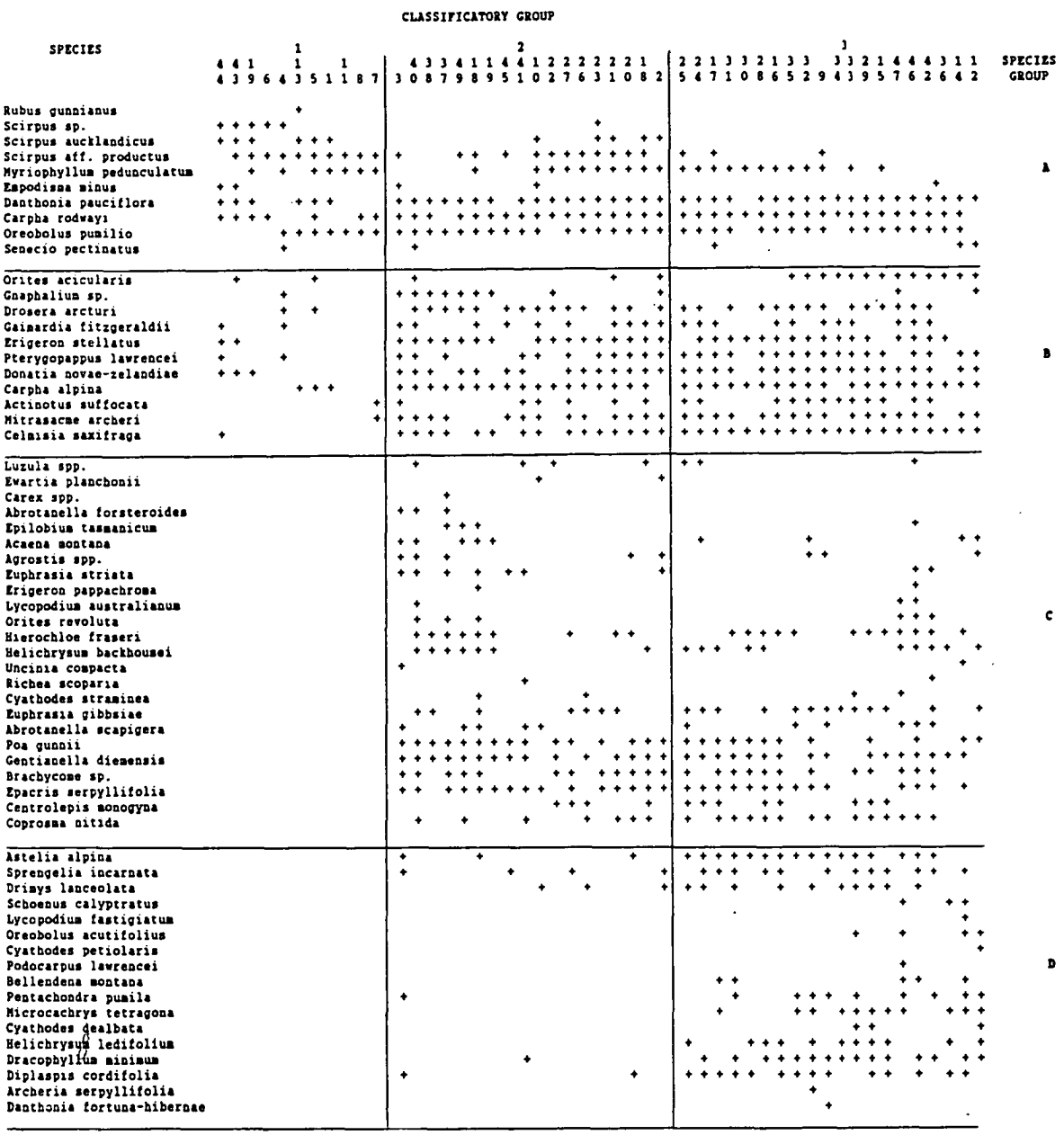
The classification of the data set revealed three intergrading groups (table 5-1), the most significant feature of which is that serial replacement of species through time is almost completely absent. The classificatory groups break the data into what is presumed to be broad age classes since tarn drainage, with group one being the youngest (i.e. newly drained, very low total plant cover) and group three the oldest (highest values of vegetation cover).

Species groups A and B arrive early in the succession followed by species group C then, at a very late stage (generally with total vegetation cover values of at least 50%) group D. Mean species number rises from 6.6 in group 1 to 24.6 in group 3. The fully re-vegetated tarns of group 3 are identical in species composition to the surrounding bolster heaths.

The ordering of species in this classification is related to soil moisture and drainage conditions. When the tarn is initially drained, the tarn floor is generally comprised of a very wet organic sludge. Three species of Scirpus are generally the initial colonizers. Scirpus aucklandicus and an unidentified Scirpus sp. are excluded in the final stage of the succession. Even when total vegetation cover is achieved some small wet areas still exist in the bolster mosaic. This is indicated by the persistence of Scirpus aff. productus and Myriophyllum pedunculatum in the oldest classificatory group (table 5-1).

Three other species show apparent replacement (Rubus gunnianus (species group A), Ewartia planchonii and A. forsteroides (species group C)). The apparent replacement of these species is most likely spurious since all three are locally uncommon on this part of Newdegate Pass. As more species invade onto these tarns, drainage becomes better. Most of the shrub species belong to species group D and arrive late in the succession. It is interesting to note that the gymnosperm Microcachrys tetragona normally arrives into a drained tarn

Table 5-1 Sorted two-way table of species by classificatory and species groups.



by vegetative spread from the surrounding vegetation. Indeed, in the entire survey only one seedling was found.

Disregarding A. forsteroides, which is uncommon in this area, the sequence of cushion plant arrival was found to be

1. Carpha rodwayi, Oreobolus pumilio
2. P. lawrencii, D. novae-zelandiae
3. D. minimum

This accords with previous observations on tolerances of cushions to water logging and the data of Kirkpatrick and Gibson (1984).

5.3.2.2 Core analysis

Analysis of the macrofossils from the core allows a much more detailed picture of past vegetation to be built up than that available from pollen records. The macrofossils found in peat are generally regarded as representing the local flora since water transport in these environments is minimal (Birks and Birks 1980, Hill and Gibson 1986a). Their interpretation relies on the assumption of similar decomposition rates for cuticle of all major species. This apparently holds for the Newdegate core given the distribution of the major species reported below.

The core was taken through a bolster heath string dam. The cushion species D. novae-zelandiae, D. minimum, A. forsteroides and P. lawrencii all occur in the present vegetation. The core was 1030 mm long. The top 90 mm consisted of a structural peat formed by enveloped cushion plant stems and leaves and, toward the bottom, adventitious roots. This section of the profile is dark reddish-brown in colour (5 YR 3/6). The rest of the profile consisted of an amorphous greasy peat of uniform brownish-black colour (5.5 YR 2/2).

Well preserved cuticle was present throughout the entire profile. Five species made up more than 99.9% of the recovered cuticle (figure 5-3). P. lawrencii and A. forsteroides were the major components while a fifth cushion plant Mitrasacme archeri, (figure 5-3) was locally abundant. D. novae-zelandiae and D. minimum appeared as minor components. Trace occurrences of an unidentified shrub species and a monocot were also recorded.

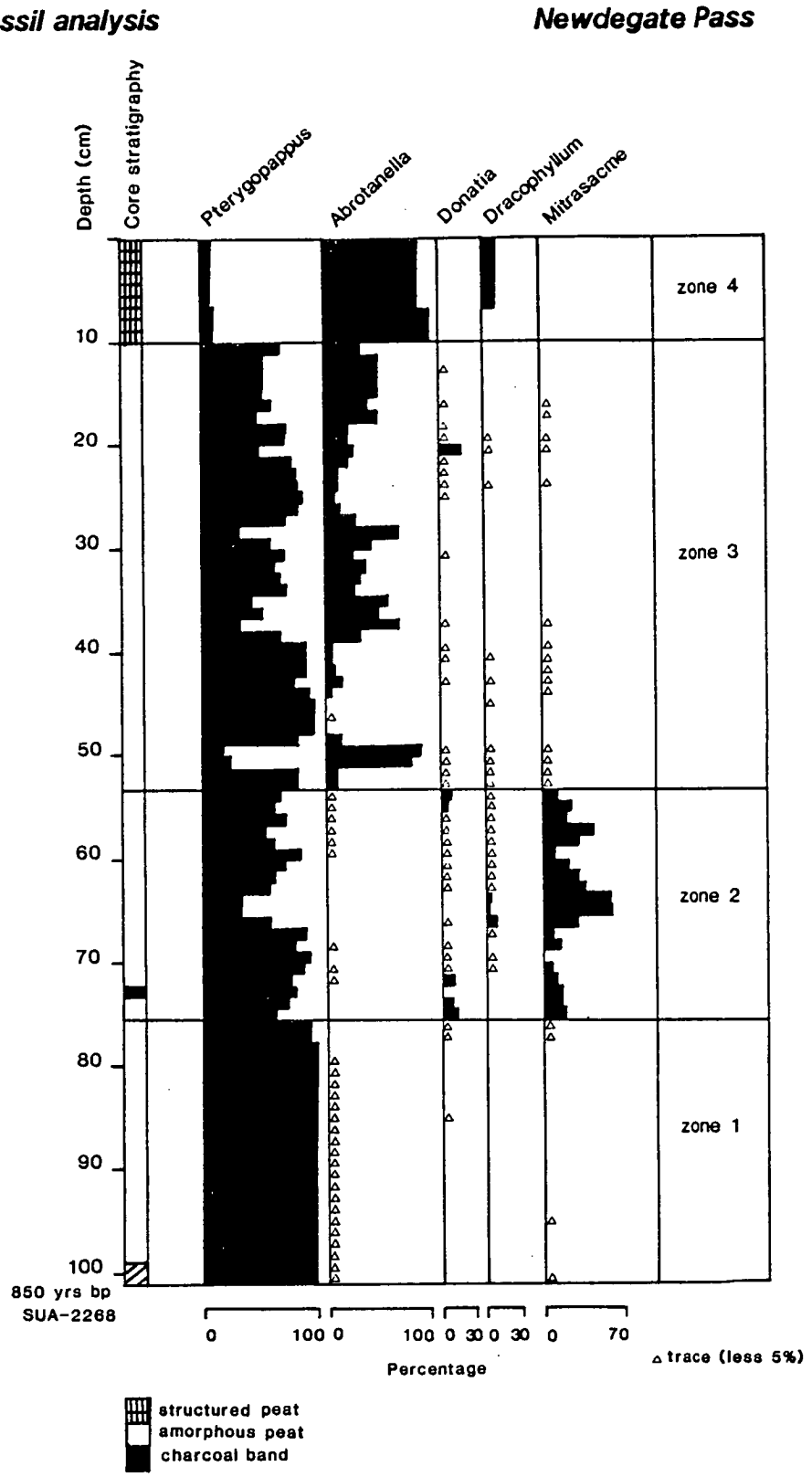


Figure 5-3 Macrofossil diagram of material recovered from a 1030 mm core from a bolster dam at Newdegate Pass.

The macrofossil profile can be divided into four zones. Zone I at the base of the profile consists almost entirely of P. lawrencii with a trace of A. forsteroides. Zone II is characterized by occurrence of the M. archeri and consistent occurrence of D. novae-zelandiae and D. minimum at low values. Near the bottom of zone II one sample had a large amount of charcoal almost co-incident with the rise in dominance of the M. archeri. Given the position of the core from a dam wall, it is unlikely that the charcoal was water transported to the site, implying that either the cushion heath or the surrounding vegetation must have been burnt at this time. In zone III both P. lawrencii and A. forsteroides are prominent with changing dominance. Zone IV is the layer of structured peat and could not be considered analogous to the rest of the profile, which has undergone significant decomposition and compaction.

The chronology of this profile remains uncertain despite a basal radio carbon date of 850 ±110 year b.p. (sample number-SUA 2268). As outlined previously, recent contamination of the sample by modern root material is possible as is humic acid accumulation above the bedrock. Further such rapid accumulation (8 years/cm) seems to contradict the measured growth rate of the cushion species (4.35-12.5 years/cm - Tasmania (table 2-5); 1.25-3.33 years/cm - in New Zealand (Bliss and Mark 1974)) given the quite significant actions of decomposition and compaction during peat formation.

Other data (Aaby and Tauber 1975, Andrews et al. 1975, Heusser 1982, Tallis 1983) suggest that a rate of peat formation under the highly humic conditions prevalent in this alpine environment, might be expected to be of the order of 30-100 years/cm. Heusser (1982) working in very similar Donatia fascicularis Forster & Forster f.peats in subalpine South America reported accumulation rates of 32-170 years/cm.

For these reasons it is suggested that this core may represent a record back to the early Holocene rather than a relatively recent profile.

5.4 General discussion

The classical successional model predicts a successive sequence of species invading a site, each more efficient in resource utilization than the last, and each modifying the environment such that it is more suitable for later seral species. This sequence leads to a stable climax community in equilibrium with

its environment. When competitive exclusion alone determines species composition there must be at least as many limiting resources as there are co-existing species (Clements 1936, Egler 1954, Cheeson and Case 1986).

This model clearly does not hold for the succession processes occurring at Newdegate Pass, given the pattern of species recruitment, the persistence of species through time and the seasonal change in competitive ranking of the dominant bolster species (Chapter 2). Community dynamics are better explained by a model of non-equilibrium processes involving both a fluctuating environment and fluctuating levels of competition (Cheeson and Case 1986).

Successional processes generally involve species replacement, even in alpine and tundra environments (Douglas and Ballard 1971, Hernandez 1973, Kirkpatrick and Dickinson 1984) such replacement seems to be largely absent at Newdegate Pass where accumulation appears to be occurring. All but the two species (Scirpus aucklandicus and an unidentified Scirpus sp. both of which require very wet conditions - table 5-1), occur in the climax vegetation. Wein and Bliss (1973) report similar results in an arctic cottongrass (Eriophorum) tussock community as do Roxburgh et al. (1988) for high alpine cushion communities in New Zealand. In these studies succession proceeds by an accumulation and change in dominance of species along the lines of the inhibition model of Connell and Slatyer (1977). Lough et al. (1987) studying the retrograde succession of a Chionochloa grassland to a cushion community also reported changes in species dominance rather than species replacement.

Data from the revegetation and core analysis at Newdegate Pass show that once a species arrives in the community it tended to persist through time. This fact and variability in both the climate and competitive rankings of the bolster species (Chapter 2) at this site indicate that competition alone is not determining species composition. Grime (1979) proposed a model for vegetation classification based on plant history strategies. Under this scheme in environments where the abiotic conditions strongly constrain productivity competition is considered unimportant (stress tolerators). Data of del Moral (1983) found however, that competition did occur in low productivity habitats. Huston (1979) proposed a similar model to that of Grime but suggested that species diversity was a function of both productivity and frequency of disturbance. In low productivity environments high diversity can be maintained by frequent disturbance (i.e. where disturbance is defined as climatic

variability) such that competitive interactions never become dominant. Such a situation appears to be occurring at Newdegate Pass.

The classical model of succession predicts that for species co-existence there must be at least as many limiting resources as species. It is difficult to intuitively accept that a high degree of resource partitioning is occurring in these environments with a very simple vegetation structure (generally only one layer) and highly organic acid peats with very low levels of available nutrients.

All discussions of community stability and competitive interactions are reliant upon an assumed time scale. Davis (1986) argued that climax communities are not stable assemblages in any meaningful sense, rather co-existence results from non-equilibrium conditions operating over relatively long periods and differential rates of change among component species. Hope (1986) and Macphail (1986) believe quite different upland associations have occurred during the Pleistocene glacial and inter-glacials than are extant today, based on pollen records. Nonetheless the climax concept is useful in discussing the vegetation at Newdegate Pass, at least on a time scale of thousands of years. Through the entire core the dominant species found are those recorded in the area today, implying that a similar vegetation has continuously occupied this site. Analysis of vegetation data from drained tarns indicates that almost all species present in the early and middle seral stages, persist in the climax vegetation. No way was found to accurately determine the time taken for complete revegetation of drained tarns, but it is likely to be in the order of 100-250 years.

The conservative calculation of a temperature drop of 5.5°C during the Last Glacial compared with the present (Kiernan 1983) would place Newdegate Pass above the snow line. Revegetation of this area probably occurred subsequent to the deglaciation of Mt. Field (c. 10,000 years ago, Macphail and Peterson 1975). It is suggested that this revegetation was likely to be by species present in the area today and that the bolster heath community is probably still expanding over block fields at the expense of the coniferous heath community. However, given the cyclical nature of the dynamics of these two communities, they are both best regarded as the climax association (sensu Churchill and Hanson 1958) of this area.

CHAPTER 6 PATTERN ANALYSIS IN MOSAIC BOLSTER COMMUNITIES

6.1 Introduction

In the previous chapter the dynamics of a bolster community was described based on plant assemblages of different presumed ages. This has been the common practice in successional studies, especially with forest successions where their youngest phases of the succession may be studied in detail while the latter stages are inferred from perceived differences in a series of older stands. The necessity of this method arises from the very long lived nature and hence slow turnover of the tree species. For a similar reason it was adopted in the last chapter in a study of the dynamics of bolster communities. The ideal situation would be to study successional processes at the one site from inception to climax, if such a community exists. There are only a few such permanent quadrats as yet established in the bolster communities in Tasmania and these plots are only five years old. The data from these plots forms the basis of the next chapter.

Another way of gaining an understanding of the dynamic processes in vegetation has been the study of pattern in plant communities and how this changes with time (Watt 1947, Greig-Smith 1952). There have been a series of methods proposed for pattern analysis including nested analysis of variance (Greig-Smith 1952), 'two term local variance' (Hill 1973) and Mead's (1974) test for independence of subplots. All these methods have serious limitations. Greig-Smith's method (and the modification proposed by Kershaw (1957) for use in line transects) has been used the most extensively (Greig-Smith 1979). Nonetheless the accuracy of the results of this method become increasingly poor at the larger block sizes due to the few degrees of freedom in their calculation. It is also sensitive to both starting position and choice of quadrat size (Ripley 1978, 1981). Mead's method is similarly sensitive to starting position and quadrat size. Hill's method suffers from problems of too few degrees of freedom at the larger block sizes (Ripley 1978, 1981).

One dimensional spectral analysis has also been used by a number of authors in the study of pattern along line transects. Ripley (1978, 1981) undertook a comparison of all four methods on a series of common data sets and concluded that it was hard to extract useful information on the presence of pattern from transects of counts. Spectral analysis seemed the most reliable although

experience was needed if misinterpretation was to be avoided. He further concluded that the results of Mead's method seemed almost impossible to interpret, while those of Hill and Greig-Smith gave variable results.

More recently two further methods of pattern analysis have been reported. A method developed by Ripley (1977) and Diggle (1979) was used by West (1984) with some success in a study on competition and pattern in Eucalyptus obliqua monocultures. This method uses fully mapped plot data and determines whether pattern is present or not by calculating departures from randomness toward aggregation or regularity. If such departure from randomness is present then a third function is calculated to quantify this departure. This method appears extremely promising but requires very large amounts of computer time (commonly 7000-10000 cpu seconds on a large PRIME mainframe computer for plots of 300 individuals). Other examples of the use of this method appear in Diggle (1983) and Ripley (1981).

The other recently reported method is two dimensional spectral analysis. Renshaw and Ford (1984) suggest this as a general interrogative technique for the analysis of pattern at a variety of scales and with the ability to detect directional components in the data. It uses a data matrix of variable size which may contain frequency, basal area or presence/absence data and produces a description of pattern using four different statistics. As yet this method appears little tried (Renshaw and Ford 1983, 1984; Ford and Renshaw 1984; Newbery et al. 1986) but appears potentially useful for a large range of vegetation data. It is also computationally simpler (c. 70 cpu seconds).

The ability of this method to use cover or dominance data makes it potentially useful in analysing pattern in cushion mosaics at intermediate levels of scale (c. 2 m x 2 m). In particular this method will be used to test the hypothesis that:

in bolster mosaic communities bolster species show continuous regeneration (i.e. all size (age) classes being present) as is apparent for A. forsteroides and P. lawrencii under conditions of non limiting resource (Chapter 4).

The mosaic bolster communities are both floristically diverse and highly complex, with three or more bolster species forming intricate mosaics. Non cushion species tend to use the bolsters as substrate and hence do not directly compete for space. It is the patterns formed by the cushions themselves that

appear to be the outcome of direct competition for space and it is by the analysis of these patterns that some understanding of the dynamics of these communities may be obtained.

6.2 Methods

The mathematical theory of two-dimensional spectral analysis is given in detail in Renshaw and Ford (1983,1984) and only a brief description of the method is given below. It is intended to examine the ecological relevance of this method in pattern analysis and not to review its theoretical base. Pattern is described by four statistics.

1) The autocorrelation function estimates the correlation between points and their successive neighbours.
2) The periodogram shows the extent to which the data contains periodicities at different frequencies.
3) The R-spectrum highlights the frequency of pattern repeats.
4) The θ–spectrum highlights directional components in the data (Ford and Renshaw 1984). Programs to compute these functions were obtained from the authors.

The periodogram produced by the analysis are generally complex and not easy to interpret so the transformation of the periodogram into the polar spectrum is used to highlight directional components and scales of pattern separately (Ford and Renshaw 1984). The directional components were analysed through the θ-spectrum which breaks the periodogram into components of approximately the same frequency angle ($-5° < \theta \leq 5°$, $5° < \theta \leq 15°$, ...$165° < \theta \leq 175°$). The scales of pattern were analysised by means of the R-spectrum which is a plot of elements with approximately the same frequency magnitude ($0 < r \leq 1$, $1 < r \leq 2$,....etc.). In the absence of spatial pattern all R and θ values have an expected value of unity (Renshaw and Ford 1984). It is possible to calculate confidence limits for each spectrum, these are normally broadest at the lowest and highest frequencies since they are calculated from small numbers of periodogram elements (Renshaw and Ford 1984).

Data sets from four plots were analysed -
Plot 1 - A mosaic cushion community dominated by A. forsteroides, and in decreasing order of importance P. lawrencii, D. minimum and D. novae-zelandiae.
Plot 2 - A mosaic cushion community dominated by D. novae-zelandiae, with P. lawrencii, A.forsteroides, Oreobolus pumilio.
Plot 3 - A mosaic cushion community dominated by D.minimum, with P.lawrencii, D. novae-zelandiae, and Oreobolus pumilio.
Plot 4 - More detail study of part of plot 2, in a area dominated by D. novae-zelandiae with P.lawrencii.

For each of the first three sites a 2 m x 2 m plot was laid out and divided into eight 0.5 x 1.0 m subplots which were vertically photographed using a 28 mm wide angle lens. Dominance of a single cushion species was later assigned to each of 1600, 5 cm x 5 cm blocks within each plot using the projection of subplot photographs onto a suitable grid. This resulted in four separate species dominance matrices of size 40 x 40 for each plot.

Two-dimensional spectral analysis can analyse scales of pattern down to twice the distance between the adjacent matrix cells (Renshaw and Ford 1984). To investigate smaller patterns of scale a section of plot 2 was analysed at a smaller scale. A 40 cm x 40 cm area in which fine scale pattern between D. novae-zelandiae and P. lawrencii occurred was selected and scored in the same method as outlined above on a 1 cm sq grid. The fourteen data sets thus generated were then analysed using two-dimensional spectral analysis.

6.3 Results

The patterns of dominance of the different cushion species are shown in figures 6-1 to 6-4 and the percentage total for each species by sites are shown in table 6-1. The periodograms resulting from the analysis of the 14 data sets were broadly similar and generally dominated by large low frequency components. The R and θ–spectra of each species at each site show overall consistent patterns with large low frequency components, the absence of high frequency components and often major directional components at 0° and 90° (figures 6-5 to 6-8).

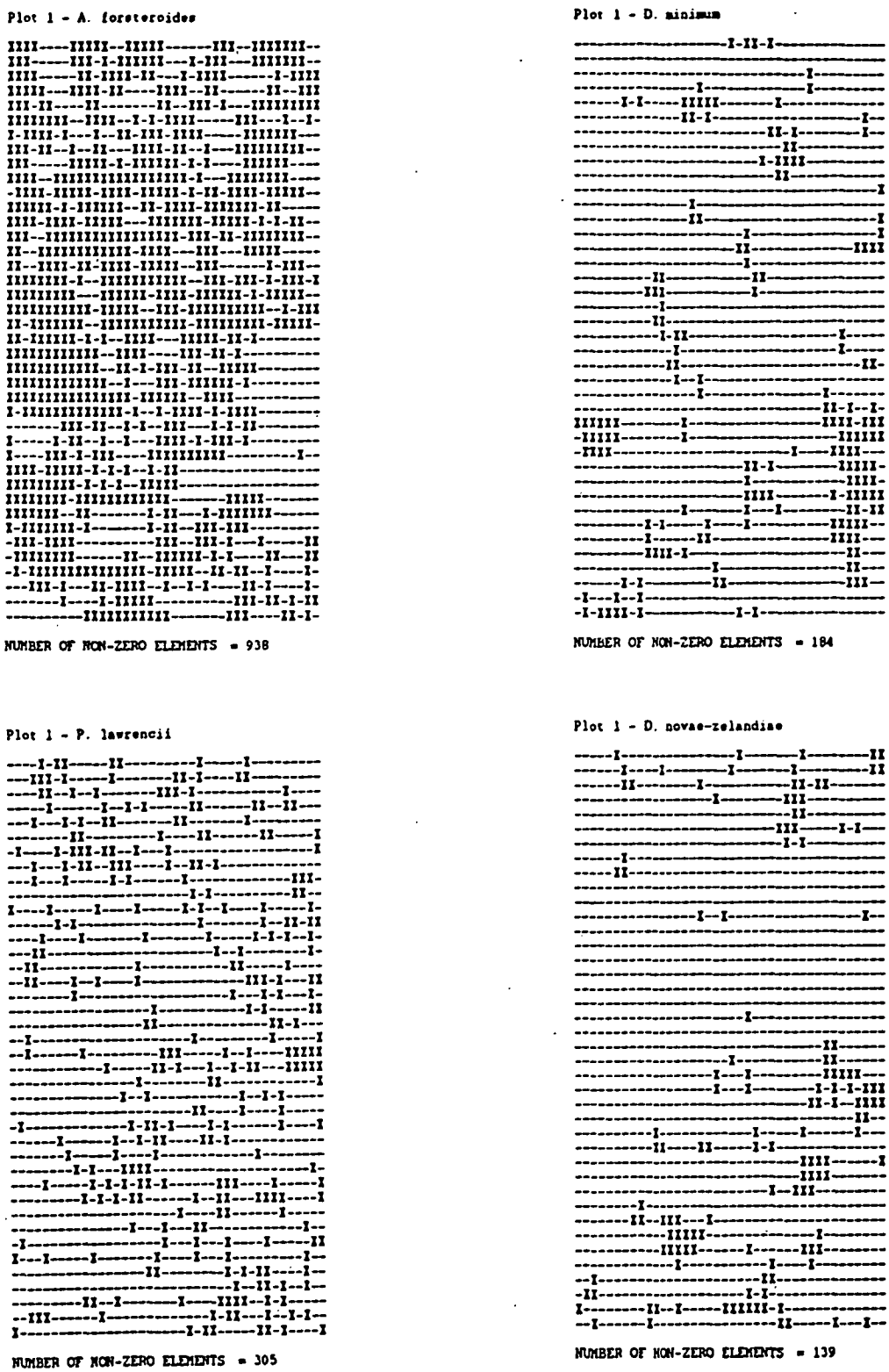


Figure 6-1 Dominant bolster species in each of the 40 x 40, five sq cm grid cells of plot 1. (a) A. forsteroides, (b) P. lawrencii, (c) D. novae-zelandiae, (d) D. minimum.

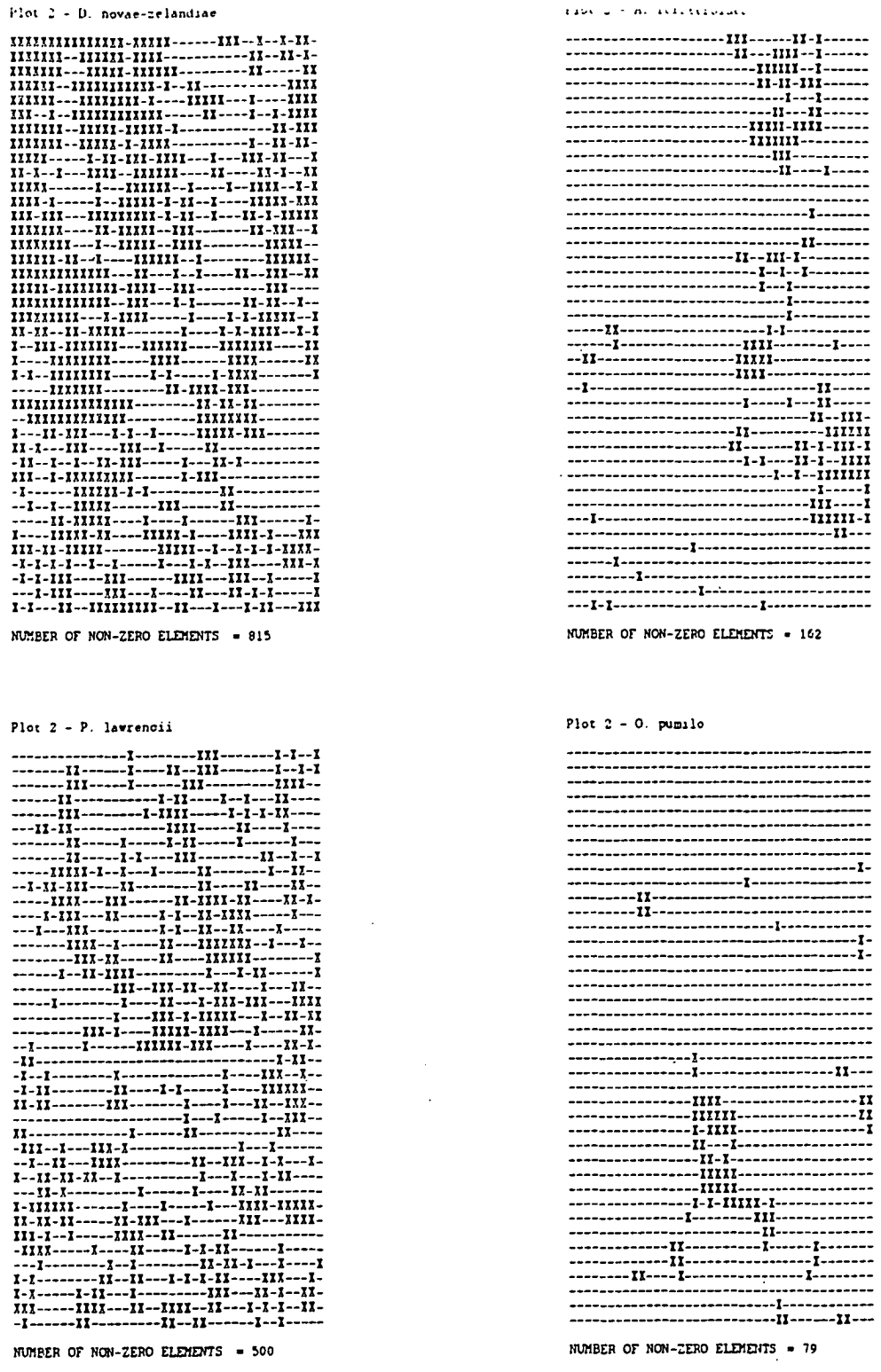


Figure 6-2 Dominant bolster species in each of the 40 x 40, five sq cm grid cells of plot 2. (a) D. novae-zelandiae, (b) P. lawrencii, (c) A. forsteroides, (d) O. pumilio.

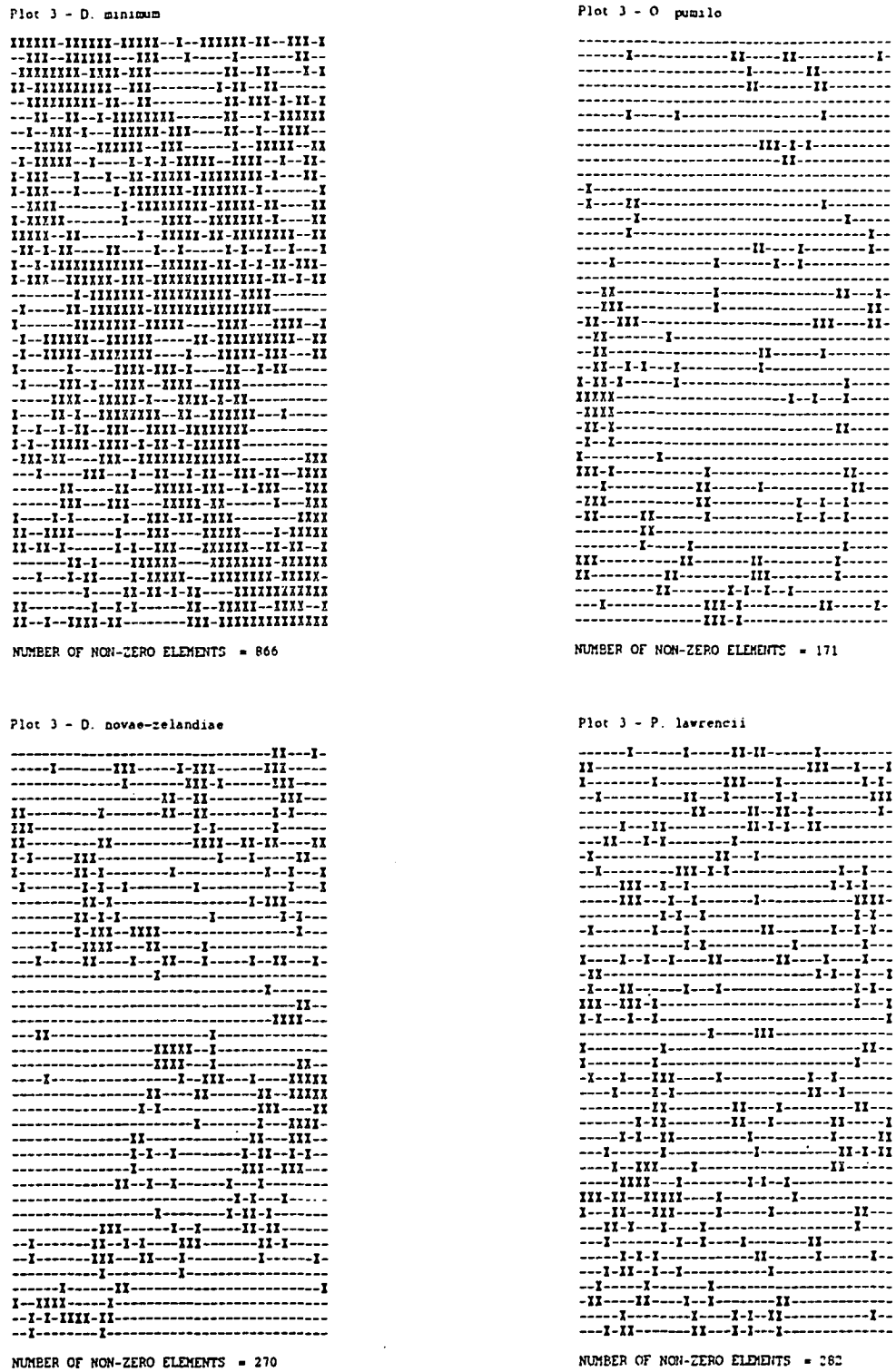


Figure 6-3 Dominant bolster species in each of the 40 x 40, five sq cm grid cells of plot 3. (a) D. minimum., (b) P. lawrencii, (c) D. novae-zelandiae, (d) O. pumilio.

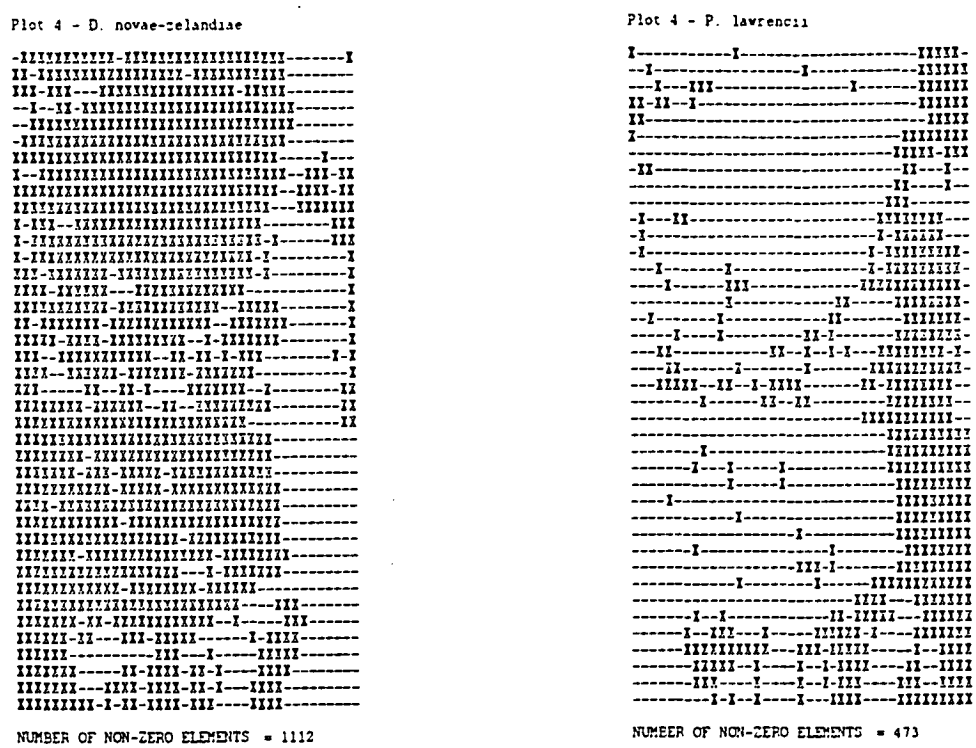
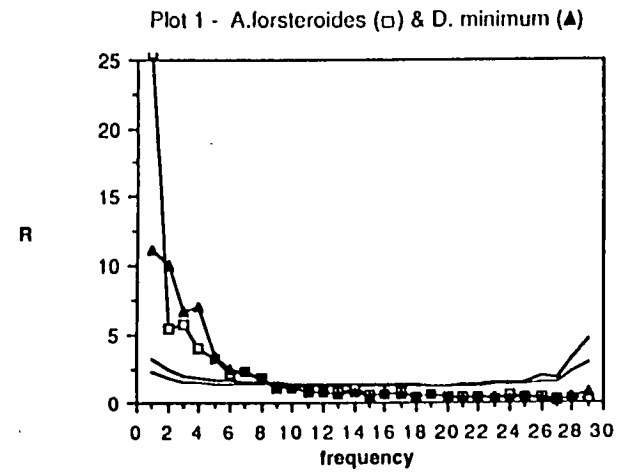


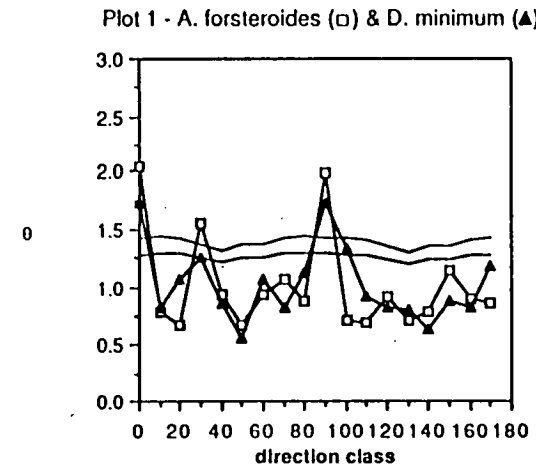
Figure 6-4 Dominant bolster species in each of the 40 x 40, one sq cm grid cells of plot 4 (a section of plot 2 at higher resolution). (a) D. novae-zelandiae, (b) P. lawrencii.

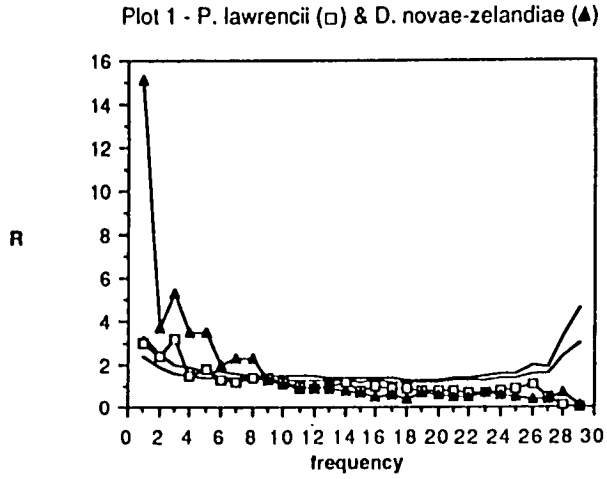
Table 6-1 Dominance of cushion species by plot. Dominance is measured as the percentage of the 1600 grid cells in which each species is dominant.

	Plot 1	Plot 2	Plot 3	Plot 4
Abrotanella	60	10	-	-
Pterygopappus	19	32	18	30
Dracophyllum	12	-	55	-
Donatia	9	52	17	70
Oreobolus	-	5	11	-

Figure 6-5 R and θ-spectra of the bolster species in plot 1. Confidence limits (0.05 and 0.01) shown as solid lines.







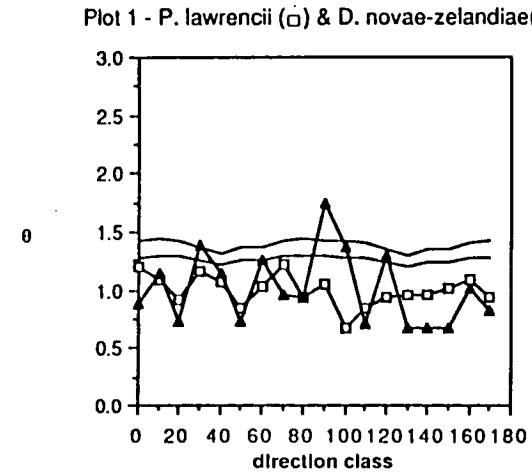
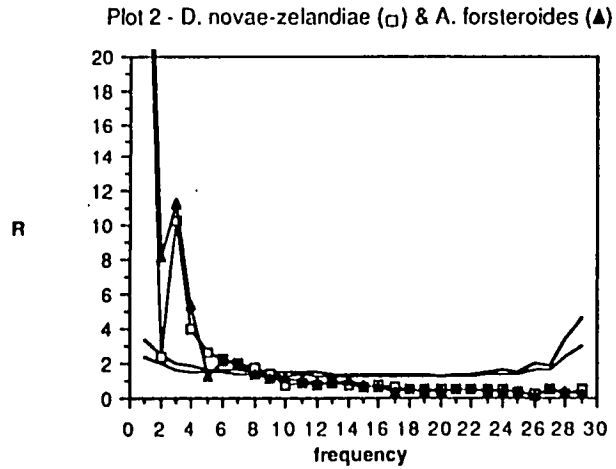
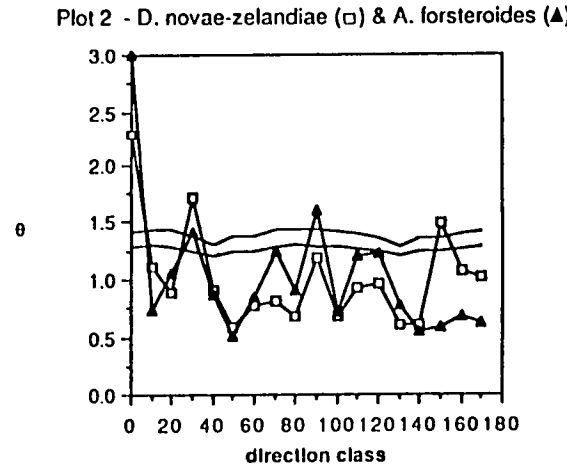
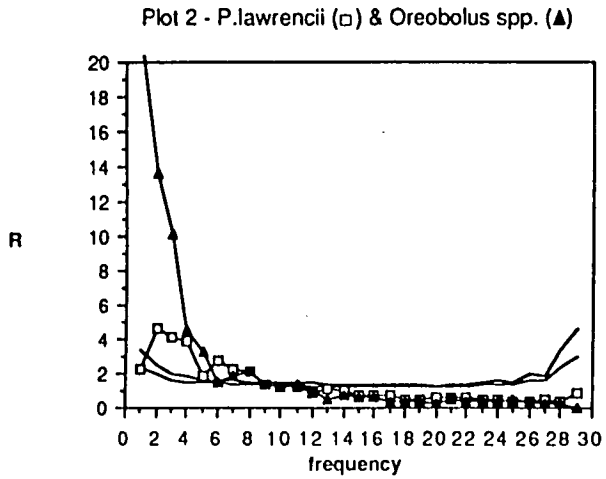


Figure 6-6 R and θ-spectra of the bolster species in plot 2. Confidence limits (0.05 and 0.01) shown as solid lines.







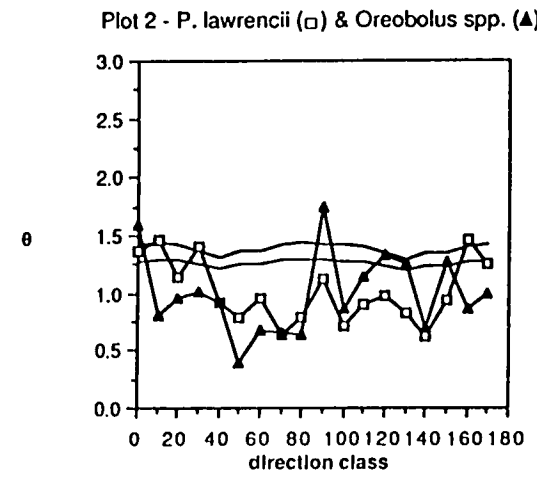
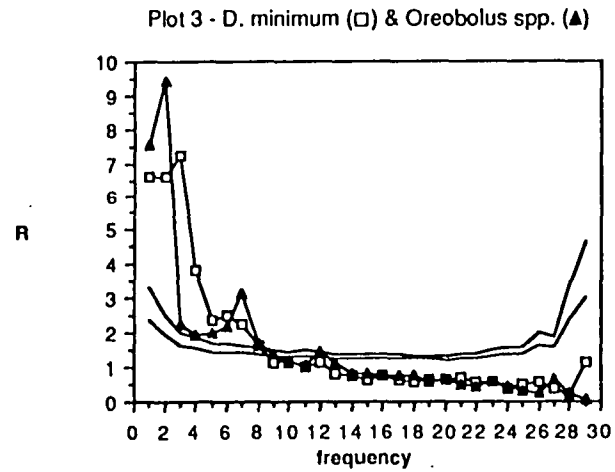
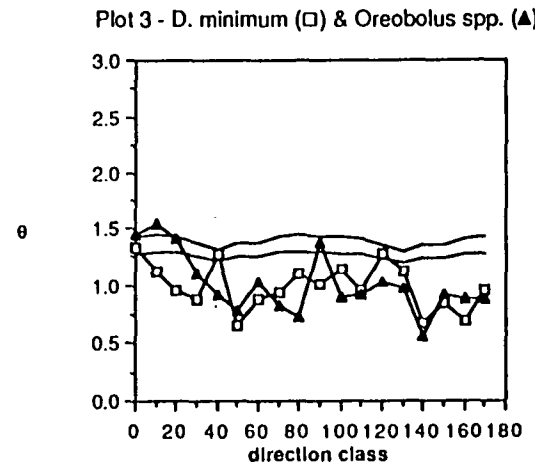
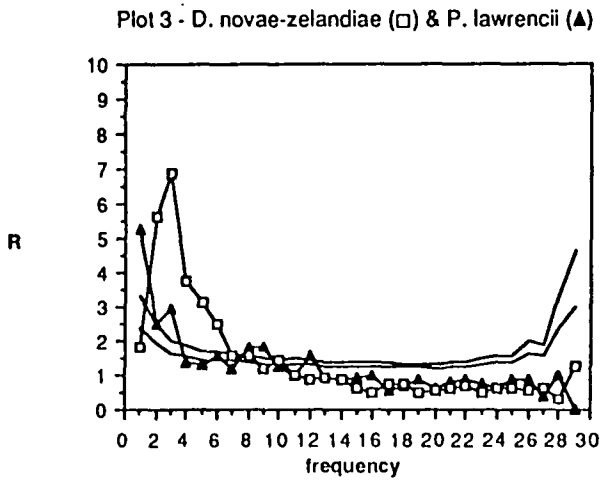
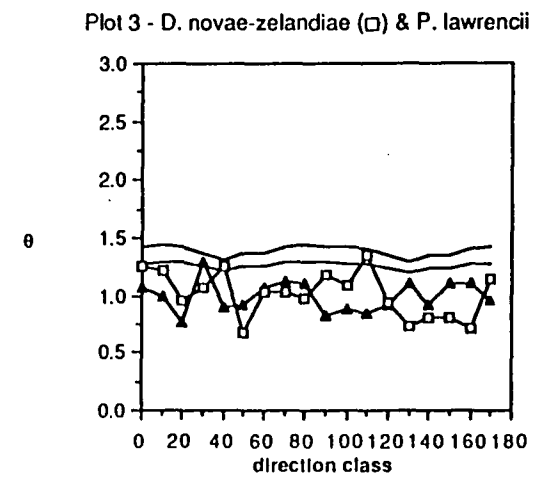


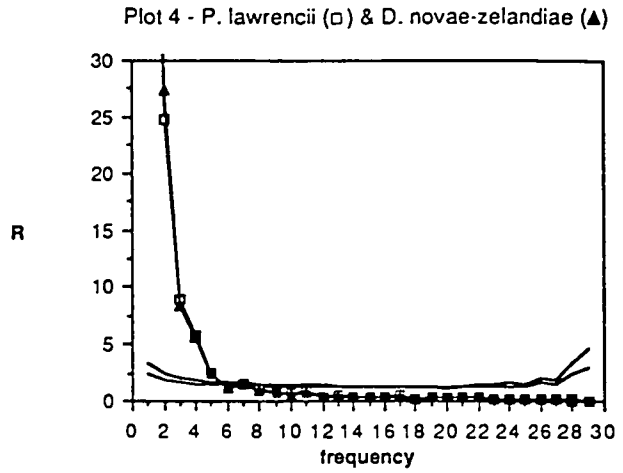
Figure 6-7 R and θ-spectra of the bolster species in plot 3. Confidence limits (0.05 and 0.01) shown as solid lines.











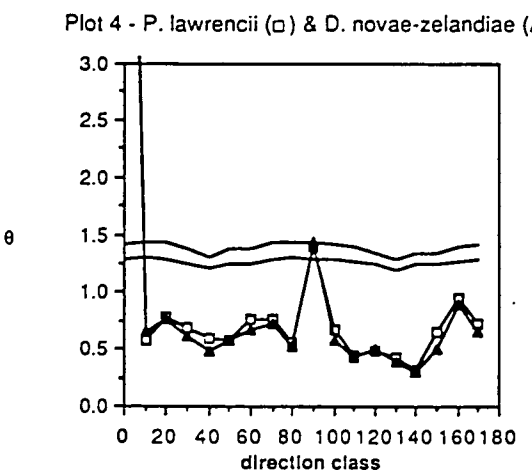


Figure 6-8 R and θ-spectra of the bolster species in plot 4. Confidence limits (0.05 and 0.01) shown as solid lines.

The data from plot 1 shows a dominance of A. forsteroides followed by P. lawrencii and similar values for D. novae-zelandiae and D. minimum (figure 6-1, table 6-1). The θ–spectra of the species in this plot show major directional components at 0° and 90°, with minor components at 30° and 120°. The R-spectra for A. forsteroides, D. novae-zelandiae and D.minimum are significant for all frequency classes (r) <9 (≤9 in case of D. novae-zelandiae).

For A. forsteroides there is a general decrease in R values for r = 1 to 8, with a minor peak in R value at r=3. The largest significant frequency class corresponds to the smallest scale of pattern in the data. This occurs at r=8 and is equivalent to a pattern of 8 cycles in 40 units (the length of the matrix), that is 5 units. Given each element in the 40 x 40 matrix corresponds to 5 cm x 5 cm grid the smallest scale of pattern identified 25 cm (40 units length/frequency of 8 = 5 units; 5 units * 5 cm/unit= 25 cm). If the dominant significant directional component was other than 0° or 90° a correction would be required.

The scales of pattern identified for A. forsteroides are ≥ 25 cm. Similarly for D.minimum there is a general decrease in significant R values from r = 1 to 8, with a minor peak at r=4 (scale of 50 cm). D. novae-zelandiae follows a similar pattern but with a pronounced peak at r = 3. All three species show strong pattern at scales ≥ 25 cm and all have strong directional component at 0° and 90°. This directional component is clearly seen in the plots of D. novae-zelandiae and D. minimum distribution which show elongated patches in both these directions.

By contrast the pattern in P. lawrencii is much less intense (as measured by significant R values), but none the less pattern occurs at r = 1, 2, 3, 5, 8 and 9. This is equivalent to scales of pattern ≥ 22.2 cm. This species shows no obvious directional component.

Pattern in plot 2 is comparable to plot 1. The dominant D. novae-zelandiae has significant R values at r = 1 to 9 as does O.pumilio, in addition this species also has a significant R value at r = 11. P. lawrencii has significant R values from r = 2 to 9. While A. forsteroides has significant R values from r = 1 to 3 and 5 to 9. Both D. novae-zelandiae and A. forsteroides show peak in their R-spectrum at r=2. D. novae-zelandiae major directional component at 0° and smaller peaks at 30° and 150°. O. pumilio has significant directional components at 0°, 90° as

well as 120°-130°. A.forsteroides is again significant at 90° and also at 30°, while P. lawrencii is just significant at 0°-10°, 30° and 160°. Again the vertical and horizontal components are dominant.

Pattern in plot 3 again shows broadly similar trends with all species showing significant R values from r = 1 to 8. P. lawrencii shows other significant R values at r = 9 and 12, D. novae-zelandiae at r = 10 and O. pumilio r = 9. This plot shows similar directional components to plots 1 and 2 but these tend to be weaker.

Plot 4 is a subplot of plot 2 analysed on a finer 1 sq cm grid. This allows resolution of pattern down to a scale of 2 cm cf. 10 cm for plots 1-3. The area of plot 2 selected for further analysis was dominated by D. novae-zelandiae with a patch of P. lawrencii along one edge and numerous small patches of P.lawrencii spread throughout the area dominated by D. novae-zelandiae (figure 6-4, table 6-1).

Pattern analysis again showed a dominance by the low frequency components, with significant R values from r = 1 to 5 and at r = 7 (equivalent to scales of pattern 5.7 cm and 8-40 cm).Strong directional components were found at 0° and 90° (figure 6-8). Analysis of the pattern in D. novae-zelandiae gave an almost identical pattern (figure 6-8).

6.4 Discussion

The scales of pattern in the data are generally seen as broad bands of significant low frequency classes in the R-spectrum. These frequency bands appear to reflect an interaction between patch size and interpatch distance. Similar results have been reported for Calluna vulgaris (Ford and Renshaw 1984). The largest significant frequency class represents the smallest scale of pattern in the data. In plot 1 A. forsteroides exhibited significant R values between r=1 to 8 (figure 6-5). The r=8 value indicates a scale of pattern of 25 cm on the significant 0° and 90° directional components, or pattern of 28.9 cm on the significant 30° directional component. (A significant directional component of 30° results in a path length across a plot of 40 units length of 40/cos30° = 46.2. This is divided by the frequency class (in this case 8) then multiplied by the grid length (in this case 5 cm) resulting in a scale of pattern of 28.9 cm).

A count of 8 horizontal and 8 vertical transects across the data matrix at 5 unit intervals gave an average number of clumps of 6 (i.e. 01..10..01..10..etc.). This would correspond to about 7 cycles on a 30° directional component. This is similar to smallest frequency recovered from pattern analysis (i.e. r=8) and suggests that the interpretation of the scales of pattern recovered are a function of both patch size and interpatch distance. Ford and Renshaw (1984) found similar occurrences of significant low frequency bands for a simulated data set (their figure 2). They interpreted this pattern as only reflecting variable interpatch distances given that in their model patch size was fixed.

The peak in the significant R-spectra of D. minimum (at r=4) and D. novae-zelandiae (at r=3) appear to reflect the mean interpatch distance between the large clumps (figure 6-1). The peak at r=3 for P. lawrencii is less easy to account for.

All above results are consistent with the interpretation of the R-spectrum showing scales of pattern which are a function of both patch size and interpatch distance. This is even more graphically shown by the analysis of the data in plot 4 where only two species were involved thus in each analysis the other species formed the interpatch space. The results of both the R and θ-spectra for both species were very similar.

In most plots significant 0° and 90° directional components were evident. Examination of individual species matrices showed that this was probably due to the elliptical shape taken on by some patches in these two directions. These elliptical shaped patches probably result from cushions being 'squeezed' by other cushion species. Such elliptical patches then exhibit a directional component along the long axis of the patch. To a lesser degree occurrence of small patches (less than or equal to three units) will generate 0° and/or 90° components due to their linear or right angled shape.

The absence of a high frequency component to the pattern of at least some of the species seems anomalous. For example visual inspection of the pattern of distribution of P.lawrencii in plot 1 (figure 6-1) seems to indicate pattern at a size of 2-3 units. This would be equivalent to a frequency class of between 13 and 20, which is not apparent in the R-spectrum.

The autocorrelation matrices produced by the analyses are a more complex representation of the data present in the periodograms, since the autocorrelations themselves are correlated (Ford and Renshaw 1984). The autocorrelations produced by the analysis of the cushion plant data sets were found to be of little use in the interpretation of the spatial pattern. Ford and Renshaw (1984) suggest that autocorrelation matrices may be of some use in the study of the shape of individual patches. In the data analysised above this was not realized since in all except the data from plot 4 the 'shapes' recovered were uniformly circular, a result not in agreement with either visual inspection or with the interpretation of the directional components in the data.

It appears therefore that the hypothesis suggesting that the cushions in mosaic communities would show continuous size class distribution is not testable using two-dimensional spectral analysis for two reasons. Firstly the scale of pattern recovered appears to be a function of both patch size and interpatch distance. Secondly the method appears to insensitive to high frequency components in the data.

A useful aspect of two-dimensional spectral analysis is the ability to test hypothesis by model analysis. Given the results and conclusions arrived at above it was desirable to test the ability of the analysis to discriminate patches of both uniform and varying sizes. To that end three models were set up. Fifty random points were generated in a 46 x 46 unit matrix. These acted as seed points for the generation of patches. Three sets of patches were generated (a) 3 x 3 unit, (b) 5 x 5 unit, (c) randomly varying patch size between 1 x 1 unit to 5 x 5 units (figure 6-9). Patches were allowed to coalesce but presence/ absence only was recorded. To test the discrimination of two-dimensional spectral analysis at high data densities the same three models were rerun using 100 random points. The central 40 x 40 matrix of each of the six data set were analysed as outlined above.

The varying patch sizes (1-5 units) were not recovered from the analysis at either packing density (figure 6-10). Both showed a minor peak at r=2 then a general decrease to r=8, all frequency classes greater than or equal to 8 being significant. The smallest significant scale of pattern thus recovered was therefore 5 units. The θ–spectra were most significant at 0° and 90° (figure 6-11). This was an artifact of patch shape. Minor peaks were also observed at

Figure 6-9 Simulation models used to test discrimination power of 2-dimensional spectral analysis. The central 40 X 40 units of a 46 x 46 matrix analysed. Clumps were allowed to coalesce.

(a) A model of 50 random squares ranging in size from 1 x 1 unit to 5 x 5 units.

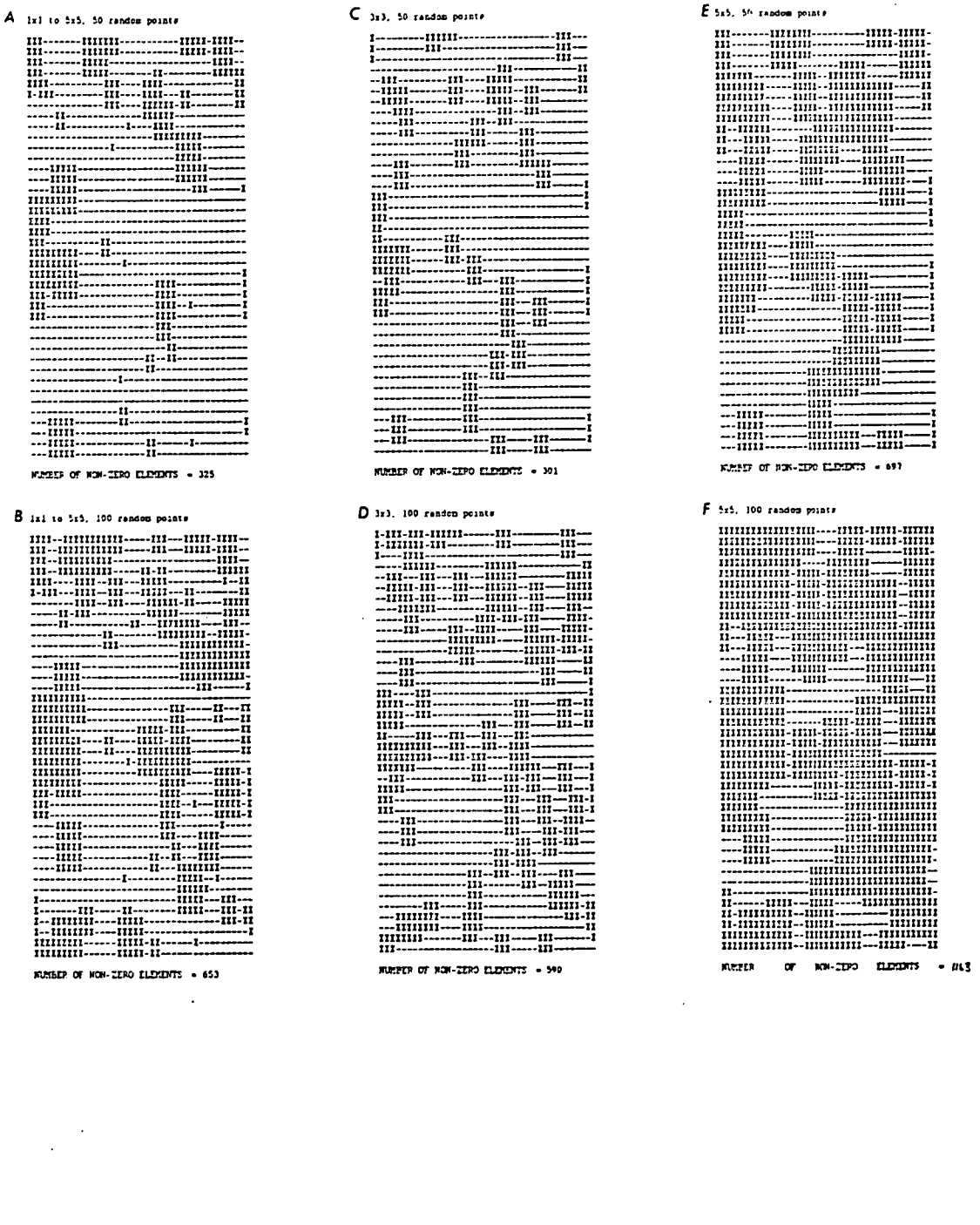
(b) A model of 100 random squares ranging in size from 1 x 1 unit to 5 x 5 units.

(c) A model of 50 random squares of size 3 x 3 units.

(d) A model of 100 random squares of size 3 x 3 units.

(e) A model of 50 random squares of size 5 x 5 units.

(f) A model of 100 random squares of size 5 x 5 units.



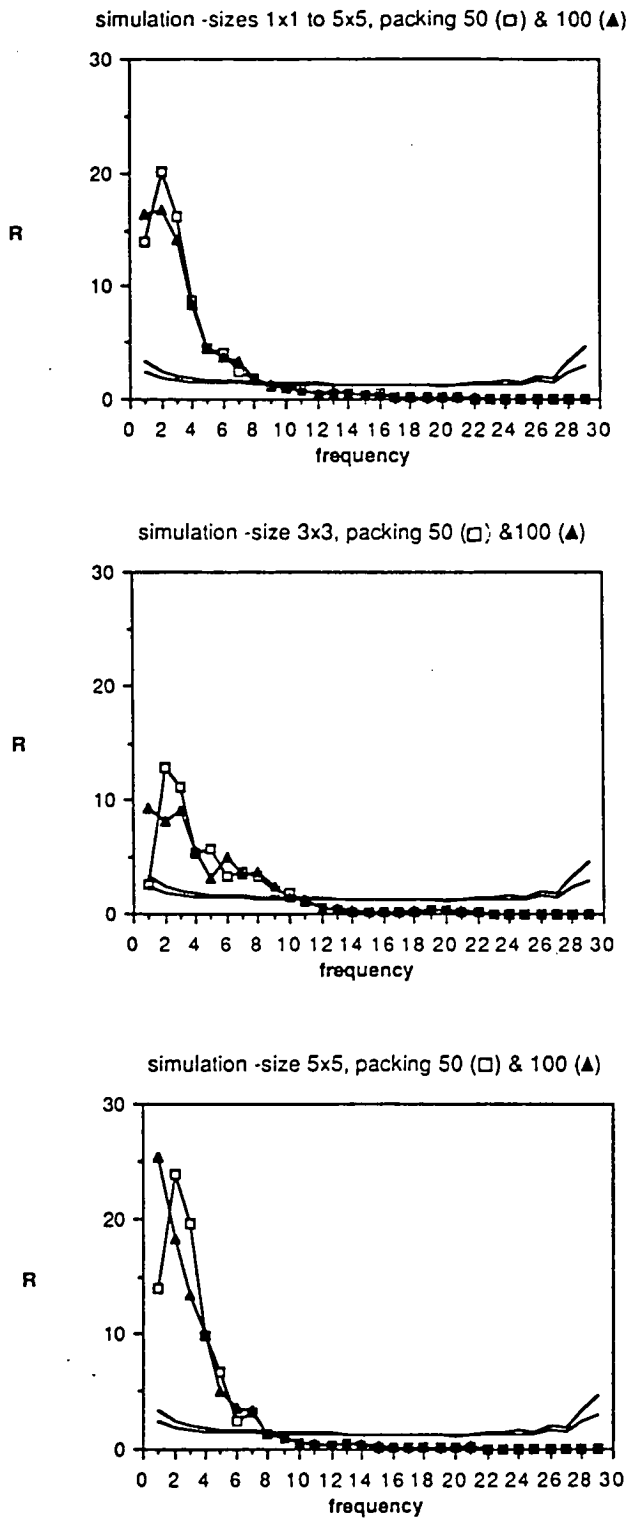


Figure 6-10 R-spectra of the six simulation models. Confidence limits (0.05 and 0.01) shown as solid lines. Results of a packing of 50 random squares are shown as open square (□) and results of a packing of 100 random squares are shown as a solid triangle (▲).

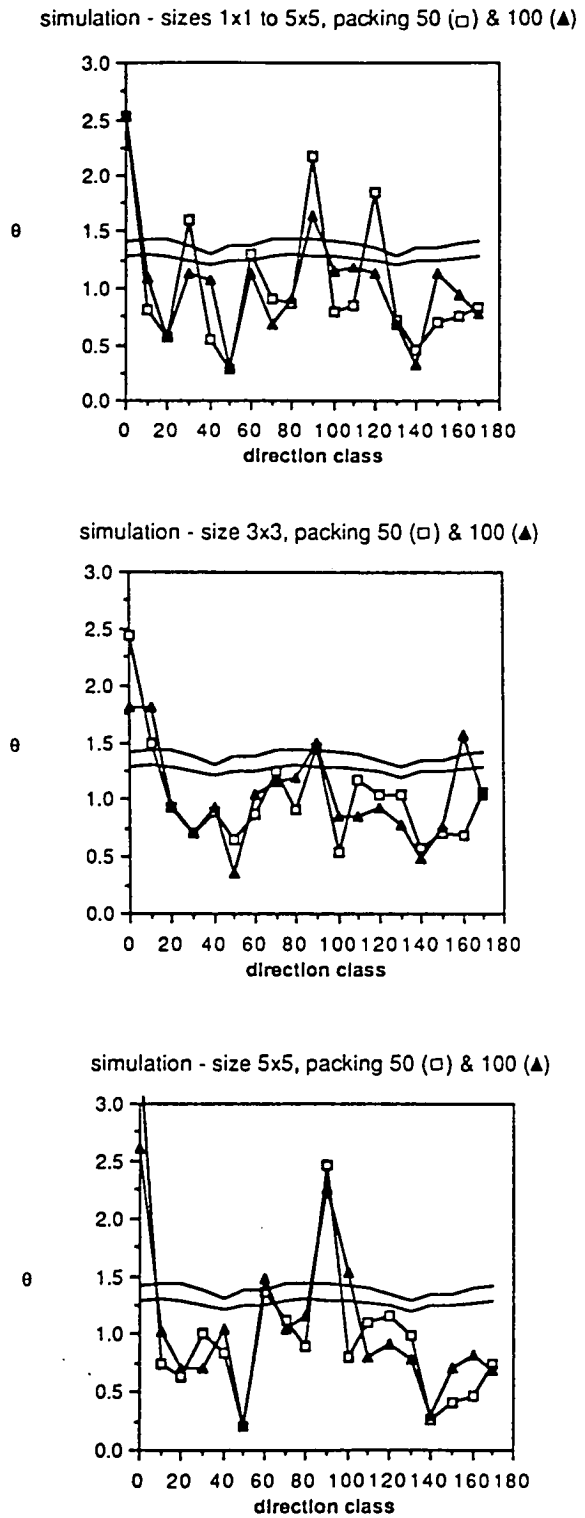


Figure 6-11 θ-spectra of the six simulation models. Confidence limits (0.05 and 0.01) shown as solid lines. Results of a packing of 50 random squares are shown as open square (□) and results of a packing of 100 random squares are shown as a solid triangle (▲).

30°, 60° and 120° at the lower packing density but these disappeared as the patches coalesced.

It appears impossible to recover a true indication of patch size from data sets in which patch size is variable using two-dimensional spectral analysis. The largest significant R value (and hence the smallest scale pattern) appears to correspond with the largest sized patch in the data.

Both packing density and size influenced the results of the even sized patches. For the 3 x 3 unit patches significant R values were found at $r \leq 10$ at the lower packing density and at $r \leq 9$ at the higher packing density. This corresponds to patch sizes of 4 and 4.4 units respectively for the smallest scale of pattern. Significant θ-spectra values occur at 0°-10° and 90° for the lower packing density and 0° and 160° for the higher. Several minor peaks are apparent in the R-spectra of both analyses and these are difficult to interpret.

The analysis of the 5 x 5 unit data set showed similar patterns although higher R values were reached for significant frequency classes ($r \leq 7$). The smallest scale of pattern recovered from these analyses was again larger than the actual patch size (6.7 cf. 5). The θ-spectra were again significant at 0° and 90° with minor peaks at 60° and 100°.

It is interesting to compare these results with a simulation reported by Ford and Renshaw (1984 - their figure 2 a,c,e). For that simulation they used a diamond shaped figure of radius one unit. This pattern is similar to the 3 x 3 unit pattern used above and Ford and Renshaw's packing density was very close to the lower packing density used above.

The results of this simulation was similar to those reported above with a broad band of significant low frequency classes. Their results did show two important differences firstly there were much better defined peaks within the low frequency band and secondly they reported a significant high frequency component. The peaks in the low frequency band were interpreted as scale resulting from both patch size and interpatch distances. These peaks were apparent in some model results (e.g. patch size 3 x 3 units at packing rate of 50) but absent from others (figure 6-10). The high frequency classes were suggested as measuring nearest neighbour distances, this feature was completely absent from all the analyses of the six different models.

It would appear therefore that two-dimensional spectral analysis is sensitive to patch size and shape and packing in the discrimination of pattern both at high and low frequencies. For models of uniform patch size two-dimensional spectral analysis appears capable of recovering a value slightly larger than the true size of the patch from the largest significant R value in the low frequency band. Peaks within this significant low frequency band may be interpretable as a function of patch size and interpatch distance. However these features are sometimes absent.

Given that this method relies on the recovery of wave patterns in the data to determine pattern scale it seems unlikely that the two components of pattern (patch size and interpatch distance) can be separated, although approximation of patch size at least appears possible for a small group of simple models. It appears therefore that two-dimensional spectral analysis is of little practical use if the components of pattern need to be determined from real data sets.

To add further qualifications to the method the question of the appearance of harmonics has not yet been investigated. Further it is not clear what significance the 0° and 90° directional components have when a significant R value occurs at r=1. In Newbery et al. (1986) it is stated that " a significant θ= 0° or 90° value is spurious when r=1 ".This fact is not eluded to in any of the three referenced papers (Renshaw and Ford 1983, 1984; Ford and Renshaw 1984) and indeed significant 0° and 90° directional components are discussed and interrupted with significant r=1 values in two examples (Ford and Renshaw 1984 - figures 1 and 2).

This method is then of only limited use in the identification of the components of pattern and as a result it is not possible to use it to test the hypothesis that pattern in cushion mosaics reflect coalescing of continuous size classes of cushions.

CHAPTER 7. SMALL SCALE DYNAMICS IN BOLSTER COMMUNITIES

7.1 Introduction

It has been suggested earlier that the community structure in associations dominated by bolsters was determined by non-equilibrium processes involving a fluctuating environment and under which competitive interactions never become dominant (chapters 2 and 5). The degree to which competition does occur in these communities has not been quantified. In order to investigate the role of competition more closely community change was monitored at a series of fixed sites over a five year period. These sites form part of a sequence of permanent quadrats established in the alpine zone at Mt. Field in 1983 which will be resurveyed at five yearly intervals.

In late 1983 permanent vertical photopoints were established in six different facies of vegetation in which bolsters were dominant or subdominant in the Newdegate Pass area. Three were established in the degenerate phase (Watt 1947) of mosaic bolster communities resulting from relatively recent lowering of the water table (estimated to have been within the last 30 years). Two were established in the building phase where cushions were apparently invading into areas of low cover and seasonally high water table, and one was established in the mature phase of an apparently stable mosaic cushion community. These photopoints were rephotographed in May 1988.

Analysis of the changes over the five year period allowed the following questions to be answered-

a) do the changes seen in the bolster vegetation conform with the model of successional pathways developed by Kirkpatrick and Gibson (1984)?

b) are competitive interactions apparent in any of the three phases of the bolster communities?

If competition plays a minor part in determining community dynamics, then little or no change should be apparent in the closed mosaic bolster community and little species replacement should have occurred in the other phases. If competition effects play a major role in determining community composition then competitive exclusion should be apparent in all phases of the bolster community.

7.2 Methods

At each of six sites (table 7-1) a series of permanent photopoints were located. At each photopoint a 35 x 35 cm quadrat was laid down and the corners marked by 30 cm steel pins. The quadrat was subdivided by fine wire into a 5 cm sq grid. Each quadrat was vertically photographed using a wide angle lens (to limit distortion) with 35 mm colour slide film on each occasion. These photographs were subsequently projected onto graph paper at scales of 1:5 to 1:1.2 depending on the level of complexity of the vegetation. The area of individual taxon (species or life form groups) was determined either by counting off graph squares or using a Tamaya PLANIX7 digital planimeter. Area figures were converted to a percentage figure to remove any slight scale errors. The differences between the percentage cover of each taxa in 1988 and 1985 were determined and these differences were analysed using a paired t-test to test the hypothesis that no change had occurred in individual species over the five year period. Where possible cushion species were further subdivided into vigorous and non-vigorous classes and reanalysed. The vigorous class was defined as having more than 80% live shoots within a patch and non-vigorous as less than 80%.

7.3 Results

The first three sites were located in degenerating cushion mosaic. This process was most advanced at site 1 located in an area above a drained tarn where the water table had dropped by 20-30 cm. At this site a dramatic decrease in P. lawrencii cover was recorded, with about half the P. lawrencii present in 1983 (37%) having disappeared by 1988 (18%) (tables 7-2 and 7-3). When the P. lawrencii is subdivided by vigour it can be seen that the vigorous class has almost entirely disappeared (20% to 2% - table 7-2). Some expansion of Carpha alpina occurred over the five years, as did the area of bare ground.

Site 2 is located in an area of cushion vegetation dominated by D. novae-zelandiae in which the water table was disrupted by the encroachment of the 1967 fire. It is not possible to give an exact date for the change in water table, since it may have resulted from erosional processes postdating the fire. However the fire gives an upper limit 21 years for the initiation of the degradation of this community. Examination of Tables 7-2 and 7-3 show a small

Table 7-1 Description of the six sites in which photopoints were established.

SITE	COMMUNITY DESCRIPTION	NUMBER OF PHOTOPOINTS
	Degenerate phase	
Site 1	Highly oxidized cushion mosaic dominated by P.lawrencii	5
Site 2	Fire damaged D. novae-zelandiae	5
Site 3	Cushion mosaic along the edge of a recently drained tarn	5
	Building phase	
Site 4	D. minimum in a soak line	6
Site 5	D. minimum at the base of a snowpatch	5
	Mature phase	
Site 6	Mosaic bolster community	3

Table 7-2 Mean total cover (%) for species/ species groups at each site in 1983 and 1988. Only taxa which occurred in at least 3 quadrats at 1 site were included. Where possible cushion species were divided into 2 subclasses, vigorous (with > 80% live shoots) and non-vigorous (<80% live shoots).

	Site 1		Site 2		Site 3		Site 4		Site 5		Site 6	
	83	88	83	88	83	88	83	88	83	88	83	88
Donatia	8.4	9.9	46.9	45.7	36.8	28.7	8.6	9.4			6.2	6.2
vigorous			10.1	3.5	32.1	16.1						
non vigorous			36.7	42.2	4.7	12.6						
Pterygopappus	36.6	18.1	13.2	20.7	13.1	24.5					29.7	28.5
vigorous	19.6	2.0	12.5	3.7	10.9	1.8						
non vigorous	16.9	16.1	0.6	17.0	2.3	22.8						
Dracophyllum					2.7	3.1	7.1	8.9	23.2	28.3	18.1	19.1
Abrotanella											38.5	39.8
Carpha alpina	0.1	3.3	6.3	17.4								
Carpha rodwayi							8.4	16.7				
Cyathodes dealbata									22.7	33.0		
Other shrubs					20.1	15.6			1.3	2.2	7.1	6.4
Empodisma minus	5.0	8.7	4.5	3.6								
Grasses			0.3	1.7					4.7	2.8		
Herbs							0.8	0.3	30.3	27.0		
Bare ground	48.0	53.9	28.5	10.4	27.2	27.7	75.1	63.5	17.7	4.4		

Table 7-3 Mean difference in cover (and standard deviations) between 1983 and 1988.Positive values indicate an increase and negative values indicate a decrease. Significant differences indicated by * for P<0.05 and ** for P<0.01. Only taxa which occurred in at least 3 quadrats at 1 site were included. Where possible cushion species were divided into 2 subclasses, vigorous (with > 80% live shoots) and non-vigorous (<80% live shoots).

	Site 1		Site 2		Site 3		Site 4		Site 5		Site 6	
	x	sd	x	sd	x	sd	x	sd	x	sd	x	sd
Donatia	1.5	2.4	-1.2	3.7	-8.1*	6.1	0.8	5.1			0.0	0.4
vigorous			-6.7	9.6	-16.0*	12.3						
non vigorous			5.5	12.8	8.0	12.6						
Pterygopappus	-18.4	16.8	7.5*	4.9	11.4**	4.8					-1.1	3.6
vigorous	-17.6*	11.8	-8.9*	6.6	-9.1*	6.4						
non vigorous	-0.8	10.7	16.4*	10.5	20.5**	7.6						
Dracophyllum					0.4	0.5	1.7	1.7	5.1*	3.9	0.9	0.7
Abrotanella											1.3	3.5
Carpha alpina	3.2	4.3	11.0	11.5								
Carpha rodwayi							8.3**	4.0				
Cyathodes dealbata									10.3	11.8		
Other shrubs					-4.5	7.2			0.8	1.8	-0.7	2.5
Empodisma minus	3.6	7.6	-1.0	2.3								
Grasses			1.4	1.3					-1.8	4.2		
Herbs							-0.5	1.1	-3.3	6.9		
Bare ground	5.9	27.7	-18.1*	11.3	0.5	3.7	-11.5**	5.6	-13.3*	6.9		

drop in total cover of D. novae-zelandiae over the sample period. More significant is the decrease in the vigorous areas of these cushions. This decline has largely been counteracted by an increase in the non-vigorous class, implying that the degeneration of D. novae-zelandiae cushions at this site is fairly slow. The loss of cover of D. novae-zelandiae cushions in the next five years may increase given that little vigorous cushion now remains at this site.

The patterns of change in P. lawrencii show an interesting contrast to that seen in D. novae-zelandiae. Over the five year period P. lawrencii has almost doubled its cover from 13% to 21%. At the same time there has been almost complete disappearance of the vigorous subclass (13% to 4%). Contemporously there has been a dramatic increase in the cover of the non-vigorous class from 1% to 17% (table 7-2). All changes in P. lawrencii cover are significant at the $P<0.05$ level. Percentage bare ground significantly decreased while there was some increase in the area occupied by Carpha alpina. It appears that with the changes in water table P. lawrencii is able to expand and occupy bare ground however this expansion may be temporary, given the decrease in vigor of this species at this site. This apparent ability of P. lawrencii to temporarily expand in areas when the water table drops may account for the dominance of the species at site 1.

Site 3 is located in a mosaic cushion community along the edge of a newly drained tarn. The exact date of drainage of this tarn is not known but the physical condition of the sides of the tarn and the health of the bolster community in 1983 suggested that it was a relatively recent event. Patterns in species change are similar to those seen at site 2. Again there has been a significant decrease in total cover of D. novae-zelandiae cushions, with a large decrease in vigorous cushions partly offset by an increase in cover of non-vigorous cushions. A significant increase in P. lawrencii was again apparent as well as a decrease in vigorous cushions. Examination of the individual maps showed the expansion of P. lawrencii occurring into areas formerly occupied by D. novae-zelandiae and Sprengelia incarnata (grouped as 'other shrubs' in tables 7-2 and 7-3). The small area of D. minimum showed little change as did the percentage bare ground.

Data from this site also show the ability of P.lawrencii to expand in areas following major changes in water table. It is not clear whether this expansion is the result from the release from suppression (i.e. competition) or

alternatively reflects a greater stress tolerance being displayed by this species. Data from site 1, which appears the most degraded, suggests that this expansion of P. lawrencii is only temporary and as oxidation of the peat soils proceeds expansion is halted and reversed. The temporary nature of this expansion is also indicated by the poor vigor seen in the cushions at sites 2 and 3 in 1988.

Two sites were sampled where cushions were actively expanding. At site 4 this occurred along a soak line with a very rocky substrate. Site 5 was situated at the base of a snowpatch on a moderate slope and well drained mineral soil. At site 4 D. minimum and D. novae-zelandiae were the colonizing bolsters while at site 5 only D. minimum occurred. These sites were considered to be examples of the early building phases of vegetation change leading to cushion dominated communities.

Along the soak at site 4 there was a small increase in cover of D. minimum. Carpha rodwayi, a flat cushion species (as defined in chapter 1), doubled in area over the five years from 8% to 17%. D. novae-zelandiae showed little change (tables 7-2 and 7-3). Percentage bare ground decreased from 75% to 64% as a result of the expansion of D. minimum and C. rodwayi.

Site 5 showed similar trends with a small significant increase in D. minimum from 23% to 28%. In three of the five quadrats the mat shrub Cyathodes dealbata was colonizing extremely rapidly. The expansion by this species largely accounts for the fall in the cover of the grass and herb groups. The expansion of the bolster and C. dealbata resulted in a significant fall in percentage bare ground from 18% to 4% (table 7-2).

At both these sites individual cushions of D. minimum were apparent. Thus it was possible to estimate the rate of lateral growth. Due to the irregular shape of some of the cushions the diameter increase was calculated from the change in area between 1983 and 1988, the results of which are shown in figure 7-1 as a plot of diameter increase against cushion diameter in 1988.

The data show a large variation in growth rate between individual cushions at both sites. At site 5 two small cushions had disappeared and 4 others showed some decrease in size. The decrease in area of the four cushions resulted from the cushions being partially overwhelmed by the mat shrub C. dealbata.

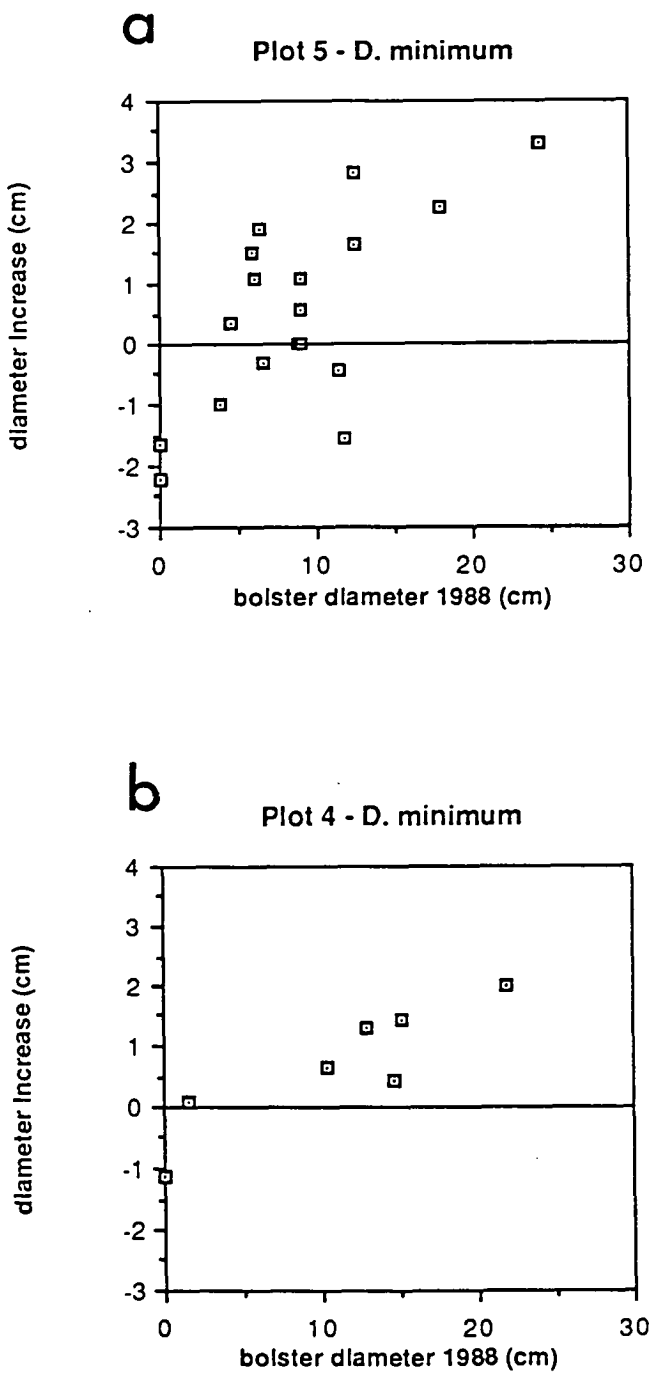


Figure 7-1 Diameter increase (in mm) of Dracophyllum minimum over the five years 1983 - 1988 plotted against diameter in 1988 (a) at site 5, (b) at site 4.

The rate of lateral growth in the remaining cushions ranged from 0-7 mm/year. There appears to be a weak correlation between diameter increase and cushion size, however the sample size is too small for much reliance to be placed on this feature. At site 4 similar patterns were found with lateral growth rates of 0-4 mm/year.

These figures are generally lower than those estimated for A. forsteroides and P. lawrencii from the study of revegetation following fire (chapter 3). At both sites reported here soil conditions are quite different. Site 4 is characterized by a largely rock substrate and little organic matter while site 5 is on a moderate slope with a gravelly mineral soils hence both would be very dry following extended periods of fine weather. In contrast all the sites sampled in the revegetation study occurred on areas of low slope and deep peat soils.

No new cushions were found to have been recruited at either site over the five year period. This may have been the result of a low intensity of sampling (as a result of quadrat size and number) at least at site 5. At this site two 10 m x 10 m quadrats were laid out and the diameters of all individual bolsters of D. minimum were recorded. The data from these plots indicate that continuous recruitment of D. minimum is occurring at this site (assuming size reflect age, figure 7-2). The soak at site 4 could not be sampled due to its small extent.

Site 6 is located in an apparently stable mosaic bolster community part of what has been referred to as the climax assemblage of the area. The vegetation pattern is highly complex (table 7-3) but in terms of total cover there is little change from year to year (total percentage cover changed by only ±2% for all species, tables 7-2 and 7-3). However detail examination of the vegetation maps show a much more dynamic situation exists than suggested by these overall figures.

In the large cushions and cushion patches (areas>0.5 cm^2) there was evidence of both degradation and expansion occurring within all quadrats. Commonly the same species was involved in the two different phases within very short horizontal distances (<30 cm). Degeneration of cushions generally involved fragmentation rather than complete death (figure 7-3), while expansion generally involved the coalescing of previously disjunct patches (figure 7-3). The coalescing of patches resulted in the minor lateral displacement of other species as did the general upward and outward growth of the entire mosaic over the five year period.

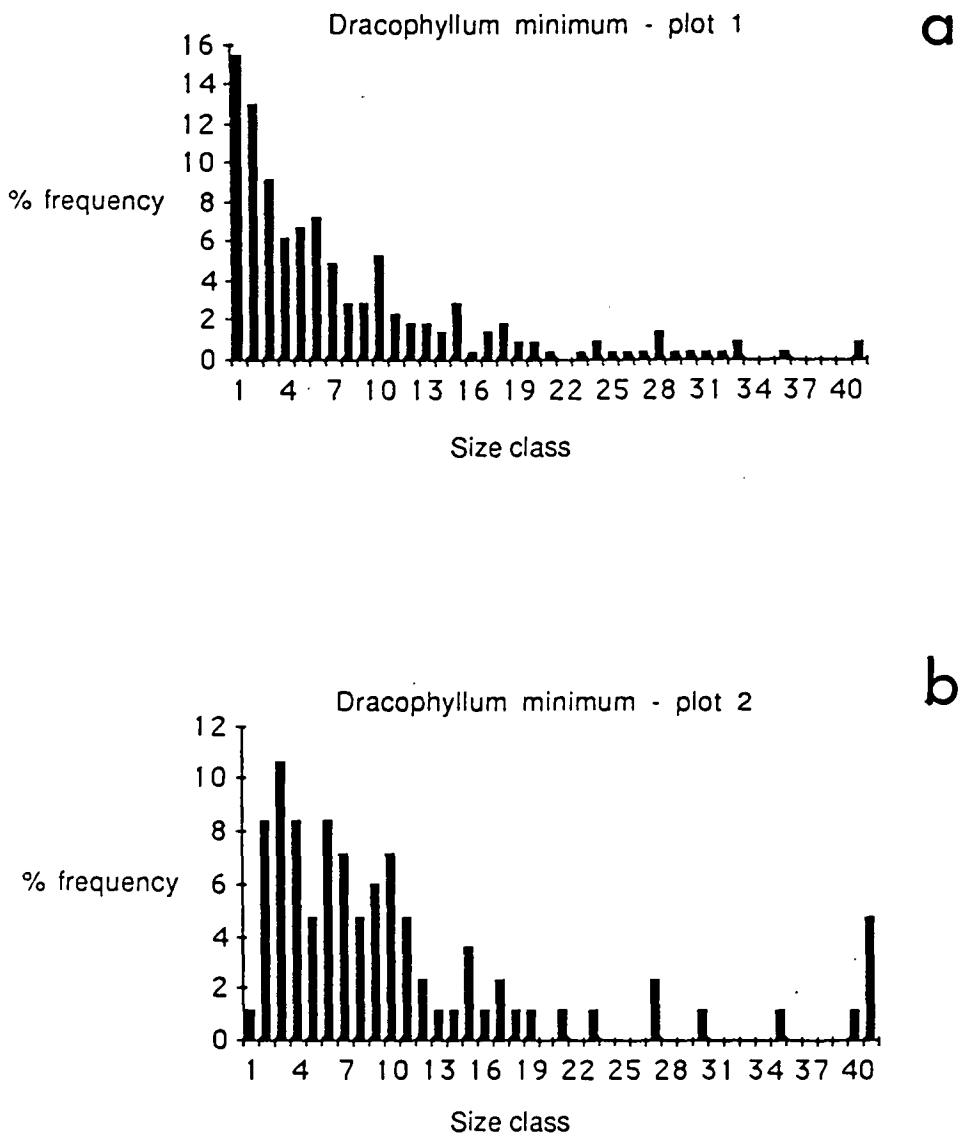
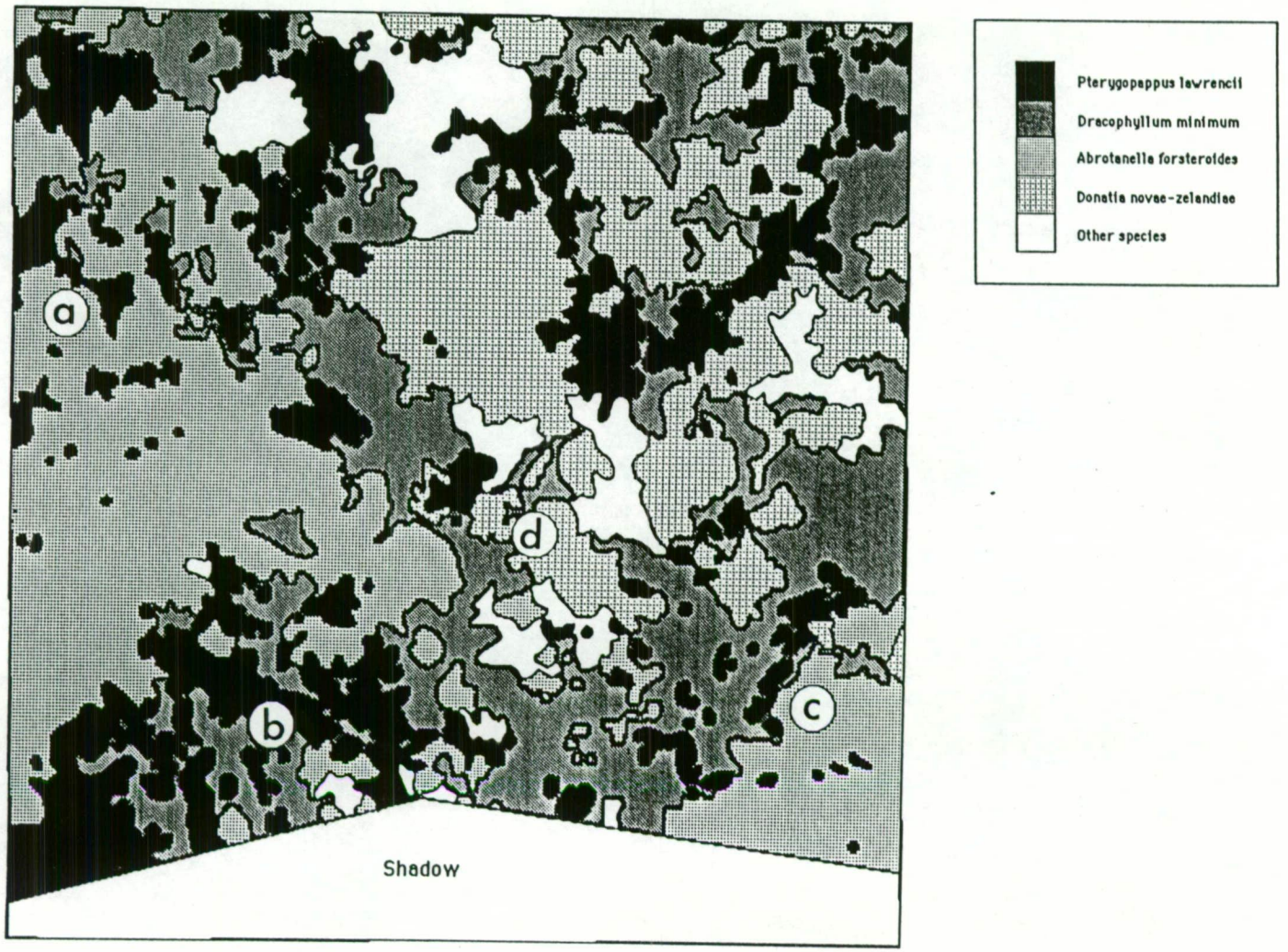


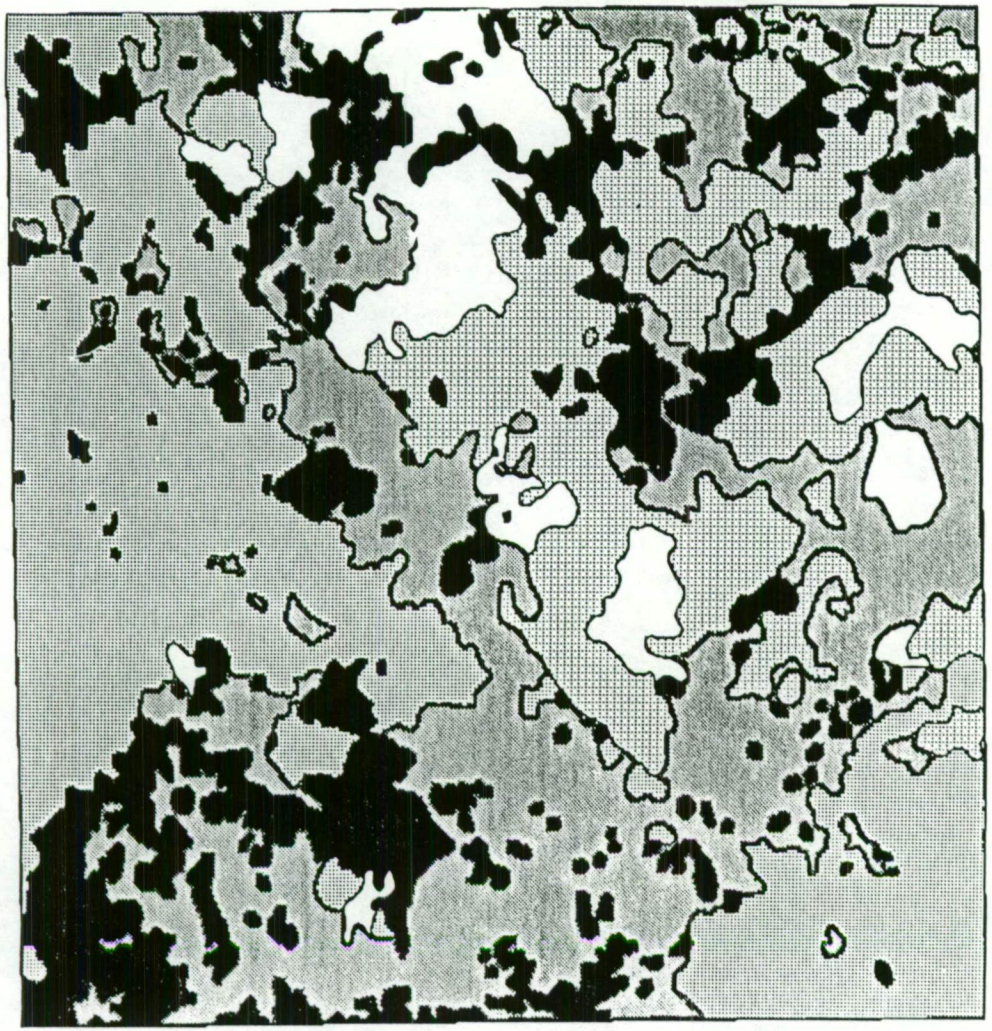
Figure 7-2 Histogram of the frequency of size classes of diameters of D. minimum cushions at site 5. Size classes are in 20 mm intervals, (a) quadrat 1, n=206, (b) quadrat 2, n=83.

Figure 7-3 Maps of the bolster species distribution of plot 1 at site 6 in (a) 1983, and (b) 1988. Plots are 35 cm square. Area labeled [a] shows fragmentation of P. lawrencii and expansion of A. forsteroides; area labeled [b] shows P. lawrencii coalescing with a subsequent loss of D. minimum; area labeled [c] shows further fragmentation of P.lawrencii; while area labeled [d] shows D. novae-zelandiae coalescing and replacing D. minimum. Also note the general lack of correspondence between the occurrence of small 'seedlings' between the two maps.

(A)


a
b
c
d
Shadow
Pterygopappus lawrencii
Dracophyllum minimum
Abrotanella forsteroides
Donatia novae-zelandiae
Other species

(B)



While dynamic changes in the larger cushions were apparent careful analysis showed equally dynamic changes occurring in smaller cushions (i.e. <0.5 cm^2 in area). Smaller individuals can arise by a variety of means including fragmentation of a larger individuals, the coalescing of other species and germination of propagules. It is not possible to assign an origin to the smaller individuals found at the first sampling. All such individuals are collectively referred to as seedlings but this term is not meant to indicate origin in this context.

Where possible the seedlings were divided into two classes, small (<0.05 cm^2 in area) and large (0.05 cm^2 <area<0.5 cm^2). Where the number of small seedlings was less than 20 no differentiation was made. By overlaying the 1983 and 1988 maps it was possible to determine seedling survival patterns (tables 7-4, 7-5, 7-6).

In quadrat 1 the seedlings of all species tended to persist over the five year period (59-74% survival) except for A. forsteroides (23% survival). P.lawrencii occurred in sufficient numbers to subdivide into small and large seedlings, with the large seedlings having a much higher survival rate (82% cf. 46% - table 7-4).

All seedlings used the older bolsters as substrate. As a result total numbers of seedlings may be underestimated since it is not possible to identify a propagule which has germinated and proceeds to grow on a bolster of the same species. It is possible to test for differential survival of the seedlings by substrate (i.e. the other bolster species or in some cases mixtures of species where seedlings are growing at the interface of two or more other species) using a X-square test. It was found that the large P. lawrencii had less than expected survival on A. forsteroides cushions ($P<0.05$) and a similar but not significant trend was found for the small P. lawrencii seedlings. No other difference was found.

Data from the second quadrat showed similar patterns. Seedlings tended to persist (68-75% survival) except for D. novae-zelandiae (survival 38% - table 7-5). A breakdown of the P. lawrencii and D. minimum seedlings into a large and small size class showed better survival by the larger seedlings (95 and 88% cf. 55 and 42% for P.lawrencii and D. minimum respectively). There was no significant difference within individual species by substrate. The third

Table 7-4 Mortality patterns of seedlings in quadrat 1 present in 1983 as percentages. Seedlings defined as individuals with an area <0.5 cm^2.

	Surviving	Dead	n
Small Pterygopappus	45.5	54.1	61
Large Pterygopappus	82.4	17.6	34
Total Pterygopappus	58.9	41.1	95
Dracophyllum	74.3	25.7	35
Abrotanella	22.7	77.3	22
Donatia	66.7	33.3	9

Table 7-5 Mortality patterns of seedlings in quadrat 2 present in 1983 as percentages. Seedlings defined as individuals with an area <0.5 cm^2.

	Surviving	Dead	n
Small Pterygopappus	55.1	44.9	49
Large Pterygopappus	95.1	4.9	41
Total Pterygopappus	73.3	26.7	90
Small Dracophyllum	41.7	58.3	36
Large Dracophyllum	88.6	11.4	44
Total Dracophyllum	67.5	32.5	80
Abrotanella	75.0	25.0	20
Donatia	37.5	62.5	8

Table 7-6 Mortality patterns of seedlings in quadrat 3 present in 1983 as percentages. Seedlings defined as individuals with an area <0.5 cm^2.

	Surviving	Dead	n
Small Pterygopappus	54.8	45.2	31
Large Pterygopappus	94.6	5.4	37
Total Pterygopappus	76.5	23.5	68
Small Dracophyllum	54.3	45.7	35
Large Dracophyllum	81.0	19.0	63
Total Dracophyllum	71.4	28.6	98
Small Abrotanella	62.5	37.5	24
Large Abrotanella	95.1	4.9	41
Abrotanella	83.1	16.9	65

quadrat similarly showed high survival of seedlings (71-83%), but again better survival by larger verses smaller seedlings and no differential mortality by substrate (table 7-6).

From the 1988 data it was possible to identify new recruitment over the five year period (table 7-7). These data are again likely to underestimate real recruitment as it is not possible to identify seedlings when they occur on cushions of the same species.

Total recruitment is similar over all three quadrats ranging from 21-38 individuals with A. forsteroides contributing the least number of seedlings and P. lawrencii showing greater recruitment (12-25) than D. minimum (6-16) except in quadrat 3 (table 7-7). There again appeared to be no substrate preference by the seedlings. There was no recruitment of D. novae-zelandiae over this period, probably reflecting the small proportion of this species present in the three quadrats. It should be noted however that recruitment is not solely dependent on the dominance, since A.forsteroides had both the highest cover values and the lowest recruitment rate (tables 7-2 and 7-7).

The figures reported above only reflect successful recruitment and take no account of mortality between 1983 and 1988. If their survivorship is similar than that recorded for the small seedlings present in 1983 then a further 50% of these seedlings could be expected to die over the next five years. Mean rate of recruitment over the five years was calculated to be 0.9/year for A. forsteroides, 1.9/year for D. minimum and 3.3/year for P.lawrencii in 35 x 35 cm quadrats. These rates (on a per unit area basis) are 1000 times higher than the figures reported for cushion species (mainly D. novae-zelandiae) from New Zealand (0.09-1.78/year in a 8 x 8 m plot - Lough et al. 1987). These differences probably largely result from the degree of precision obtainable in 35 cm square quadrats compared with an 8 m square plot. Despite these differences successful recruitment in both areas is low to very low on an annual basis.

7.4 Discussion

The patterns of change seen over the five year interval are in broad agreement with the successional pathways suggested by Kirkpatrick and Gibson (1984) from a study of spatial variability within bolster communities which was

Table 7-7 Patterns of recruitment of seedlings originating between 1983 and 1988 at site 6 by species and quadrats. Counts in normal text; rate of increase (individuals/year) in bold text. Quadrat size 35 x 35 cm.

Species	Quadrat 1	Quadrat 2	Quadrat 3	Mean
Pterygopappus	25	12	13	16.7
	5.0	**2.2**	**2.6**	**3.3**
Dracophyllum	6	6	16	9.3
	1.2	**1.2**	**3.1**	**1.9**
Abrotanella	1	3	9	4.3
	0.2	**0.6**	**1.8**	**0.9**
Total	32	21	38	30.3
	6.4	**5.2**	**7.6**	**6.1**

assumed to reflect different ages. This study of five years of change at fixed locations allows the Kirkpatrick and Gibson model to be refined.

It was assumed by Kirkpatrick and Gibson (1984) that the entire five hectares of bolster dominated community at Newdegate Pass started from a series of small disjunct individual cushions growing on a rocky substrate. The patterns of change at the two sites of recent cushion invasion (sites 4 and 5) demonstrate such establishment is currently occurring on a small scale. At these sites competition appears to be much less important than environmental stress. The mapped quadrats show that death of several of the smaller cushions was not a result of any competitive effects (sites 4 and 5). Likewise the lateral growth rates of these small individual cushions was both slow and highly variable (figure 7-1), their growth rates largely reflecting the prevailing microenvironments.

The period of time necessary for the establishment of closed cushion communities is not known, but the growth measurements in the building phase suggest that this takes considerable periods. The exact length of time would depend on density and spatial arrangement of seedlings and recruitment rates and patterns.

With the development of closed communities the cushion species largely generate their own more hospitable substrate. In the revegetation study following fire (chapter 3) much greater lateral growth rates were reported for cushion species growing on flat peat substrates (6.7-20.0 mm/year) than are apparent for the cushions colonizing the extreme sites reported here (0-7 mm/year).

With the gradual closure of the cushion vegetation and the associated raising of the water table, severe environmental stress (e.g. summer drought) decreases in importance as a determining factor of community composition. At this stage (as exemplified by site 6) competitive interactions are apparent but are largely restricted to the smaller individuals. For these small individuals mortality exceeds 50% over five years but this decreases rapidly with increasing size. This implies that once an individual has reached a sufficient size to ensure an adequate resource base then it becomes very difficult to displace. Within the stable mosaic there is dynamic change with some cushions fragmenting and others rapidly filling the available space. These changes are

largely in balance and no shifts in species dominance are seen. The cause of this restricted large cushion mortality is not clear, it may result from competition or from individual senescence. The mosaic bolster communities appear highly stable provided there is no change in water table and may occupy sites for very long periods (chapter 5).

If the water table is lowered by the drainage of a tarn down slope or the encroachment of fire into the cushion peat, the mosaic bolster community begins a degradation sequence which ultimately results in the transition to an alpine heath or low coniferous heath. Sites 1-3 show the early stages of the degradation process. The time frame for this transition from necrotic bolster to alpine heath has not been determined. It appears that during the first 20 years (dated from the 1967 fire at site 2) there is a gradual decrease in the vigor of the cushion species leading to their eventual death. The exception to this general trend is P. lawrencii which appears to initially be able to expand into available space following the lowering of the water table. It is not clear whether this results from a release from suppression (i.e. competition from other species in the mosaic) or an innate ability to tolerate drier conditions. This expansion appears to be temporary.

Site 1 appears to be the most degraded and the peat has oxidized to some depth. The P. lawrencii at this site showed a large significant decrease in cover.The degradation appears to be continuing with a significant increase in bare ground, only a small expansion of Carpha alpina and Empodisma minus and an almost complete absence of shrub cover. An extended time period is obviously necessary for the stabilization of this site. Site 2 appear to be stabilizing more quickly given the significant increases in cover of C. alpina but again no shrubby element was present. The drop in water table appears to be much less than that at site 1 and this may influence both degree and depth to which the peat oxidizes and consequently the time period to achieve the community transition.

In the degradation phase the abiotic factors (e.g. degree and depth of peat oxidation, occurrence of germination sites, summer soil moisture conditions, etc.) once again appear to be more significant than competition in determining community composition.

In broad terms the changes observed in the three phases of the bolster communities appear to fit the model proposed by Kirkpatrick and Gibson

(1984). The sites studied do not sample the transition from necrotic bolster to alpine heath/ low coniferous heath. It is possible these transitions may occur at sites 1, 2 and 3 at a later time. The sites presently under study do not sample the transition from the heath communities to bolster communities nor the pool transitions. Studies of these aspects would justify the placement of further photopoints.

Competitive interactions are apparent in the mature phase and perhaps in the early degenerative phase while in the building and mid-degenerative phase abiotic factors appear to be much more important in determining community composition. Even in the mature phase competitive interactions are generally confined to small individuals (areas<0.5 cm^2)while between the larger individuals these interactions are weak or absent.

In terms of successional theory the bolster communities appear to fit the non-equilibrium models with fluctuating levels of competition such as proposed by Huston (1979) where disturbance would be defined as a variable alpine climate. Equally Connell and Slatyer's (1977) inhibition model fits if a slight modification is made to account for the difficulty in the establishment of the bolsters. Clearly the equilibrium models fail to account for both the lack of pioneering species in the secondary successions (chapter 5) and more importantly the lack of strong competitive interactions seen in the different phase of the bolster communities.

CHAPTER 8 THERMAL PROPERTIES OF CUSHION PLANTS.

8.1 Introduction

The third section of this thesis (chapters 8 and 9) looks at the functional significance of the cushion form. In particular the thermal properties of cushion plants are examined and a comparison of the anatomical structure of four cushion species is undertaken.

The development of the cushion form has long been believed to be related to the ability of compact cushions to absorb and store radiation and to the resistance to mechanical injury conferred by the cushion shape (Moseley 1877, Bliss 1962, Wace 1965). Spomer (1964) considered that the cushion growth form was controlled by temperature. But given the wide range of environments in which cushion plants occur, it is unlikely that this is the sole cause for the evolution of this lifeform. Nonetheless the ability of the cushion form to absorb radiation is likely to be very important in some environments (Seppelt and Ashton 1978, Longton 1970).

Turner (1981) studied the insulating properties of A. forsteroides at subzero temperatures. She was able to show that A. forsteroides was an extremely efficient insulator and concluded that this growth form effectively protected roots from the short term subzero temperature experienced in the Tasmanian alpine environment. Her studies on the effects of subzero temperatures on seedlings showed 100% survival at temperatures of -1° C for 8 hours but 0% survival at -10° C for 4 hours. She concluded that the cushion form was important for the protection of roots in the mature plant and that some loss of seedlings was likely during rare periods of extended severe subzero temperatures.

Using these data as a starting point, two questions were asked -

a) what is the rate of freezing of mature cushions of D. novae-zelandiae, D. minimum and A. forsteroides and the peat soil in which they grow, and what consequence do these data have in relation to survival of adult plants at subzero temperatures in the field?

b) what is the root freezing temperature of D. novae-zelandiae, D. minimum, A. forsteroides and P. colensoi and what consequence does this data have to seedling survival in the field?

The rate of freezing of mature P.colensoi was not examined given the restricted nature of this species in Tasmania and the destructive nature of the experiment.

During the course of the growth experiments (Chapter 2 and appendix 3), the data from the temperature integrators indicated that cushion surface temperatures were considerably above the ambient temperatures. Close interval temperature data was collected for the cushion species A. forsteroides and Azorella selago from contrasting environments to determine the thermal characteristics of these cushions in the field.

8.2 Methods

8.2.1 Freezing experiments

Thirty centimetre diameter cushions of A. forsteroides, D. minimum and D. novae-zelandiae were collected from Mt. Field, taking care to avoid root damage. A peat soil block approximately 30 cm x 30 cm x 15 cm was also collected from the same area. The cushions were packed in vermiculite in plastic trays, and kept under artificial light at c.15° C. The cushions and the peat block were at field capacity at the time of the experiment.

Each of the cushions and the soil block were in turn placed in the freezing chamber. The freezing chamber allowed variable cooling rates to be applied and final temperature was held to within ±1° C. A nine channel Grant recorder was used to measure air temperature and cushion temperature at depths of 1.5 cm, 3.0 cm, 4.5 cm 6.0 cm, 7.5 cm, 9.0 cm and 10 cm. The recorder was initially set to 15 minute intervals then extended to hourly intervals once all probes had reached 0° C. The cooling rate was set at -0.2° C/minute to a final temperature of -10° C. The experiments were run for approximately 40 hours.

Root freezing temperatures of the four species were determined using 10 to 15 small pieces (c.5 cm) of live root to completely surround a thermistor sensor. Five such probes were then placed in the freezing chamber and cooled at -0.5° C/minute. Root freezing was determined by the exogenic heat loss due to liquid

phase change (Burke et al. 1976). Material was collected in February and stored at 4° C at field capacity.

Three months old A. forsteroides seedlings growing in a peat soil (under 4° C and 24 hour photoperiod) were subject to the following temperature regimes:

- 5° C for 2 hours(16 seedlings)
-10° C for 2 hours(15 seedlings)
-15° C for 2 hours(17 seedlings)
- 2° C for 7 days (56 seedlings)
- 5° C for 7 days (52 seedlings)

Seedlings were then removed to a 10° C environment and left for 1 week after which the percentage survival of seedlings was determined. Shoots and roots of both live and dead seedlings were then separated and dried at 105° C for 24 hours. Dry weights were then determined.

8.2.2 Field experiments

Temperature data were collected at hourly intervals for 10 days from 12-21 January 1985 on Mt. Wellington. A nine channel Grant recorder with fine probes (<1 mm diameter) was used to measure air temperature (shielded), the temperature inside an A. forsteroides cushion at depths of 0.5 cm, 2.5 cm, 7.5 cm, and 12.5 cm and in the adjacent soil at depths of 2.5 cm, 10 cm, 20 cm and 30 cm.

Similarly, temperature data were collected from an Azorella selago cushion at Perseverance Bluff on subantarctic Macquarie Island over a 48 hours period at half hourly intervals during 6-8 December 1985 (for site description see appendix 3). Cushion temperatures were recorded at depths of 0.5 cm, 2.5 cm, 5.0 cm and 7.5 cm while soil temperatures were recorded at depths of 5.0 cm, 10.0 cm and 20.0 cm. In both cases the probes were inserted in the middle of the cushions to minimize the effect of sun angle (Fischer and Kuhn 1984).

8.3 Results

8.3.1 Freezing experiments

Root freezing temperature varied between -1° and -2° C in A. forsteroides, D. minimum, D. novae-zelandiae and P. colensoi (table 8-1). Unpublished data of Hill and Turner (pers. comm. 1981), using the same technique show root

Table 8-1 Root freezing temperatures (°C) in A. forsteroides, D. minimum, D. novae-zelandiae and P. colensoi, mean of five replicates.

	Freezing temperature
A. forsteroides	-1.0° ± 0.3°
D. minimum	-1.4° ± 0.6°
D. novae-zelandiae	-1.2° ± 0.8°
P. colensoi	-1.6° ± 0.5°

freezing of A. forsteroides to occur at a somewhat lower temperature (-4.6° ± 0.2° C). No information is available on when this material was collected, under what conditions it was stored or its soil moisture status. The difference in temperature response may be related to seasonal or genotypic variation or to root turgidity. All species are, nevertheless, stress avoiders (Levitt 1972). D. novae-zelandiae, P. colensoi and A. forsteroides lack a persistent tap root. The depth of occurrence of the live root layer is variable in these species but generally occurs from 6 to 15 cm below the cushion surface (figure 8-1). D. minimum on the other hand has a persistent tap root, so that the depth at which roots occur depends on cushion age. In young seedlings root depths may be at 0.5-1.0 cm whilst in mature cushions, the depth at which roots occur may be greater than 50 cm.

Mature cushions of all three species are extremely effective thermal insulators (table 8-2), A. forsteroides and D. minimum being more efficient than D. novae-zelandiae. This difference is probably due to the smaller size and consequent denser packing of the shoots of the two former species (shoot densities are shown in table 2-5).

The temperature profiles from this experiment were essentially similar for all species and only the profile for A. forsteroides is shown here (figure 8-2). Temperature drop was rapid in the surface layers of the cushion, but the rate of cooling fell rapidly with increasing depth. Once O° C was reached, temperature dropped only slowly to -1° to -2° C, until complete freezing had occurred, when a faster cooling rate was once more apparent.

The peat soil block had a slower initial cooling rate than the cushions, probably due to its amorphous nature. Freezing occurred at approximately -1° C at all depths. This resulted in a lapse of almost 9 hours before the temperature started dropping below -1° C at 1.5 cm depth (table 8-2).

Root freezing did not commence in A. forsteroides for 9.5 hours (i.e. the time the top of the root layer (approx. 6 cm) reached 0° C) or in D. novae-zelandiae for 6.3 hours (table 8-2). The low temperatures necessary to achieve these conditions are very rare in the Tasmanian alpine zone. Temperature integrator data from Mt. Field West show that temperatures of between -5° and 0° C were reached for significant periods of time in June, July, August of 1984 at depths of 7.5 cm into the cushions (figure 2-7). However at no stage were

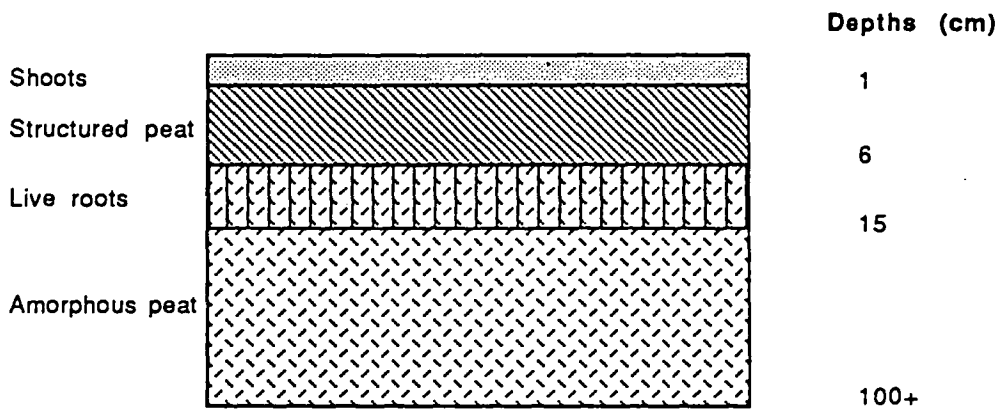


Figure 8-1 Zone diagram through an Abrotanella forsteroides cushion, live roots are generally found concentrated between 6 and 15 cm depth.

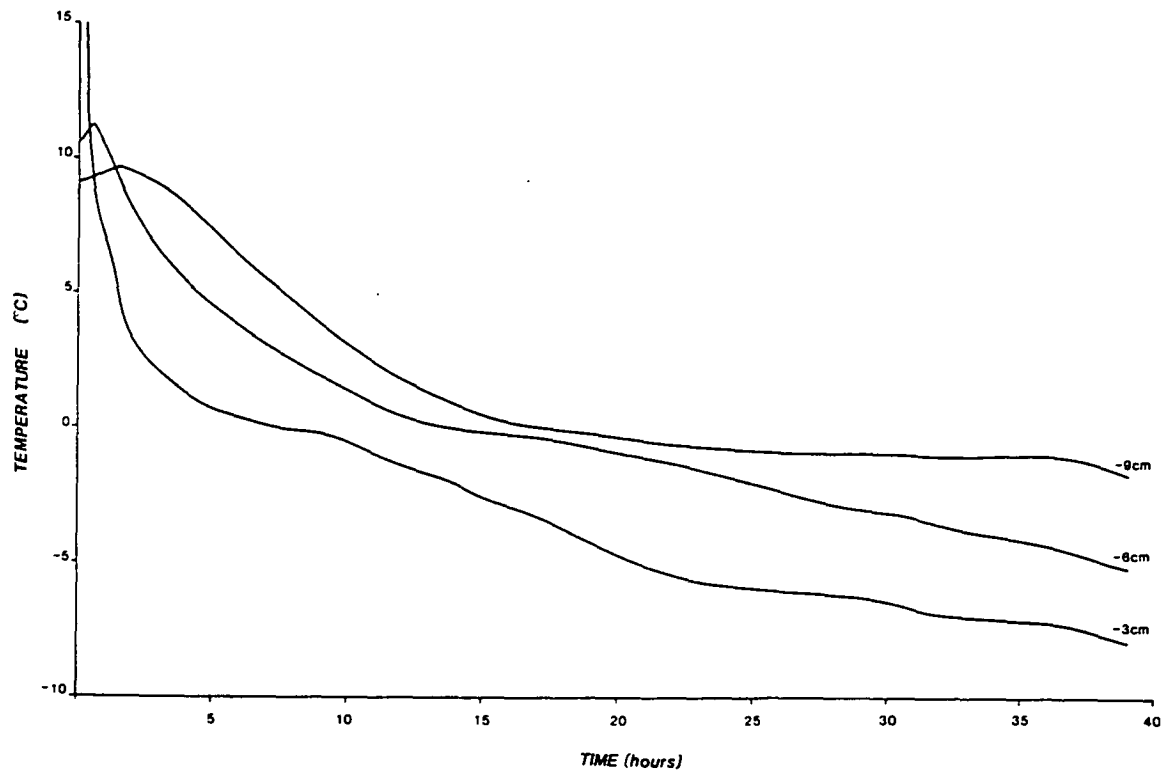


Figure 8-2. Temperature profiles at depths of 3, 6 and 9 cm in an A. forsteroides cushion when subject to a -10°C environment.

Table 8-2 Times (hours) taken to reach 0° C and complete ice formation and temperature after 40 hours in a -10° C environment at seven depths (in cm) for three bolster species and a peat soil block.

				Abrotanella			
Probe depth (cm)	1.5	3.0	4.5	6.0	7.5	9.0	10.0
Time to 0° C	4.0	7.0	11.3	13.0	15.5	16.8	*
Time to ice formation from 0° C	5.0	3.0	4.8	9.5	15.5	21.0	*
Temperature after 40 hours	-8.0°	-7.9°	-6.8°	-5.1°	-3.3°	-1.8°	*

				Dracophyllum			
Probe depth (cm)	1.5	3.0	4.5	6.0	7.5	9.0	10.0
Time to 0° C	2.0	4.5	6.8	10.3	13.3	14.3	13.8
Time to ice formation from 0° C	3.5	5.8	4.5	4.8	13.8	25.8	31.3
Temperature after 40 hours	-9.8°	-9.0°	-8.1°	-6.0°	-2.9°	-1.3°	-1.3°

				Donatia			
Probe depth (cm)	1.5	3.0	4.5	6.0	7.5	9.0	10.0
Time to 0° C	1.3	2.3	6.0	8.8	10.5	10.5	10.8
Time to ice formation from 0° C	2.3	5.5	6.3	6.3	13.5	15.3	19.8
Temperature after 40 hours	-11.8°	-11.7°	-10.6°	-9.2°	-7.5°	-7.3°	-6.3°

				Peat soil block			
Probe depth (cm)	1.5	3.0	4.5	6.0	7.5	9.0	10.0
Time to 0° C	5.0	8.8	11.3	11.3	14.0	11.0	14.8
Time to ice formation from 0° C	3.8	4.3	10.0	10.3	16.5	14.5	29.0
Temperature after 40 hours	-9.1°	-7.0°	-5.9°	-6.9°	-4.1°	-6.0°	-1.3°

* indicates probe failure

temperatures of less than -5° C recorded, and given the extended period of time necessary for phase change (table 8-2) it is unlikely that root freezing ever occurred.

Given that peat soil has even lower thermal conductivity than cushion plants (as can be seen from table 8-2), it could be expected that seedling death due to rare periods of extended severe subzero temperatures would be low in peat soils, contrary to the suggestion of Turner (1981).

This hypothesis was borne out by the results of a series of freezing experiments carried out on A. forsteroides seedlings grown on a peat soil (table 8-3). The lowest temperature of -15° C for 2 hours is probably a more severe condition than would generally occur in alpine Tasmania except perhaps in frost hollows. Seedling death was minimal at -5° C and -10° C and rose to 24% at -15° C (table 8-3). On thawing, the root systems of the dead individuals were discoloured and flaccid, a condition consistent with death by freezing. The dead individuals had significantly lower number of shoots, shoot dry weight and root dry weight than the surviving seedlings ($P<0.05$, Mann-Whitney U test), indicating that the less vigorous individuals are more susceptible to freezing damage.

The extended trials on A. forsteroides seedlings were carried out assuming root freezing temperatures of -4.5° C (Hill and Turner pers. comm.). Over 7 days, little death resulted with the -2° C environment, while 77% of seedlings died in -5° C environment (table 8-3). Again the surviving seedlings were significantly more vigorous (shoot number $P<0.01$, shoot and root dry weight $P<0.05$, Mann-Whitney U test). These results imply a root freezing temperature of between -2° and -5° C (cf. -1° to -2° C, table 8-1). The growth of these seedlings for an extended period at 4° C before the commencement of the freezing experiment may have resulted in significant hardening to low temperatures. This may be the reason for the different results obtained between the root freezing temperature determinations and the seedling freezing experiments.

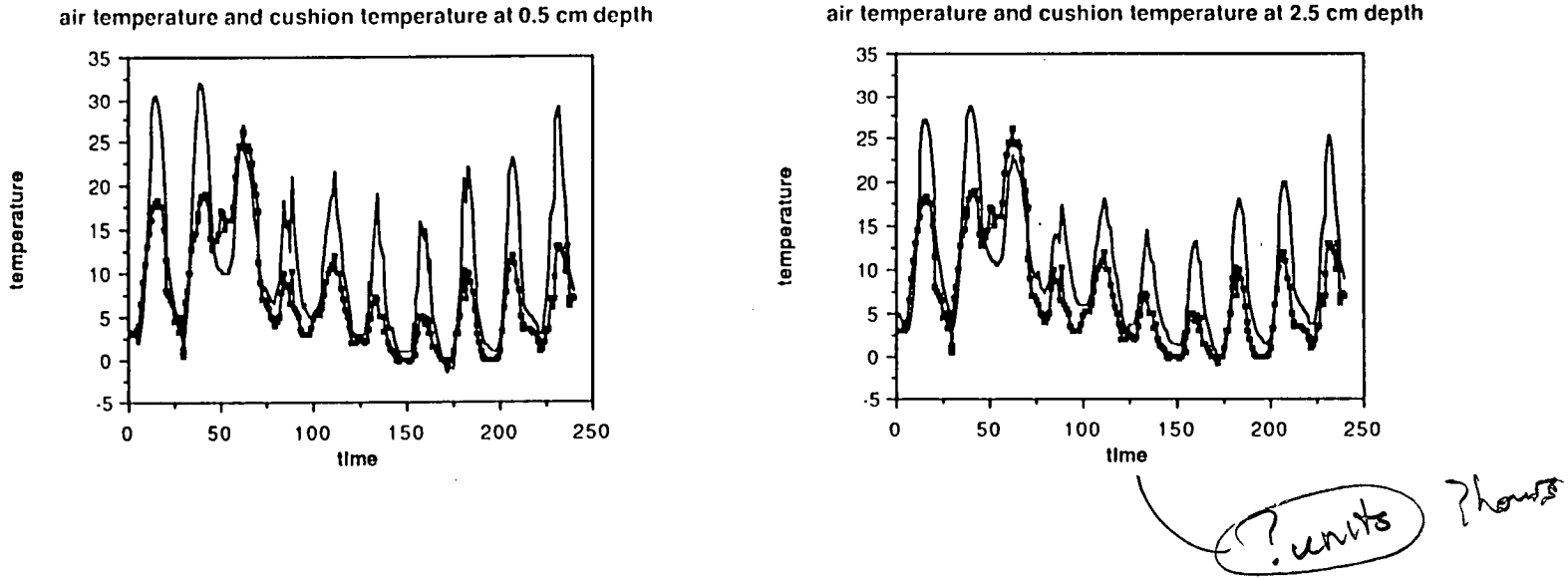
8.3.2 Field experiments

The measurements of air temperature and cushion surface temperature made on Mt. Wellington over a 10 day period are shown in figure 8-3. The weather

Table 8-3 Temperature, time and percentage survival of A. forsteroides seedlings following freezing (n = number of seedlings).

Temperature	Time	% survival	n
- 5° C	2 hours	88	16
-10° C	2 hours	87	15
-15° C	2 hours	76	17
- 2° C	1 week	96	56
- 5° C	1 week	23	52

Figure 8-3 Air and cushion temperatures at different depths between 12 - 21 January 1985 at the Mt. Wellington site, air temperature shown by solid boxes (■) and cushion temperature by a continuous line (__).



conditions were variable over this period. The only direct environmental measurement made on the site was shielded air temperature. A reasonably accurate picture of the weather conditions at this site can be constructed from available meteorological observations (The three hourly observations of air temperature, wind speed speed, cloud cover, height of cloud base, weather observations and air pressure at Hobart, 5 km east and 1200 m lower than the site; and the eight hourly upper winds report and the 9 pm aerological measurements collected by balloon above Hobart airport some 15 km east of the site).

The Hobart temperature curve closely follows that of Mt Wellington but is generally some 3°-5° C warmer (figure 8-4a). The first three days were generally fine and warm, becoming hot on the third day. High level pre-frontal cloud was apparent on day 2 and, with the crossing of the front on day 3, thickened and shower activity was reported on days 4, 5, 6 and 7.(figure 8-4b,c). Cloud cover decreased after this period. While the wind speeds were generally light and variable in Hobart (<20 knots) they were somewhat stronger at altitude (figures 8-4a and 8-5a) nonetheless winds were generally light during the period of shower activity following the passage of the front. Using the 9 pm aerological measurements of air temperature and dew point from the balloon data it is possible to estimate the extent of cloud thickness (i.e. levels of atmospheric saturation), these data show a thick cloud layer was present on days 4-6 consistent with the weather observations (figure 8-5b and 8-4b).

While not being a direct measure of the conditions prevailing at the Mt Wellington site the general influences are clear. The pattern changed from generally fine and clear conditions on the first few days to a period of thickening high level cloud to showers and low cloud with the passing of the low pressure system. Wind speed could be expected to be generally light and variable except during the passage of the front. The mountain remained completely immersed in cloud from day 4 to day 7 after which the cloud base rose and cloud cover decreased. Some strengthening of the wind was likely in this latter period. Although Hobart only recorded 6 mm of rain considerably more could be expected to have fallen on the mountain.

The most obvious feature of the temperature records collected on Mt Wellington (figure 8-3) was the consistently higher temperature of the cushion surface

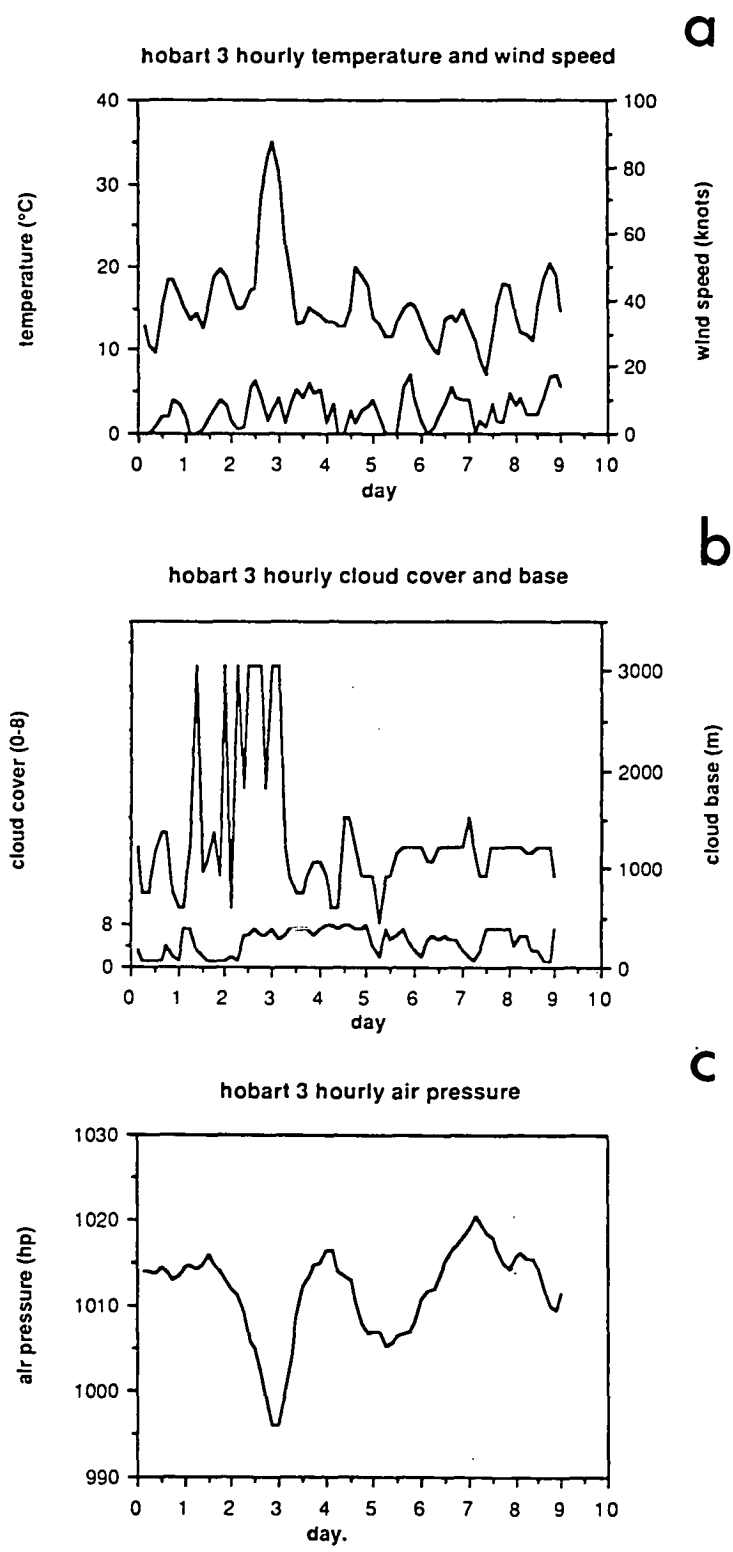


Figure 8-4 Meteorological observations in Hobart from 12 - 21 January 1985.

(a) Hobart three hourly temperature and wind speed. (Upper curve, temperature; lower curve, wind speed).

(b) Hobart three hourly cloud cover (from 0 (cloud free) to 8 (complete cloud cover) - lower curve) and cloud base (upper curve).

(c) Hobart three hourly air pressure.

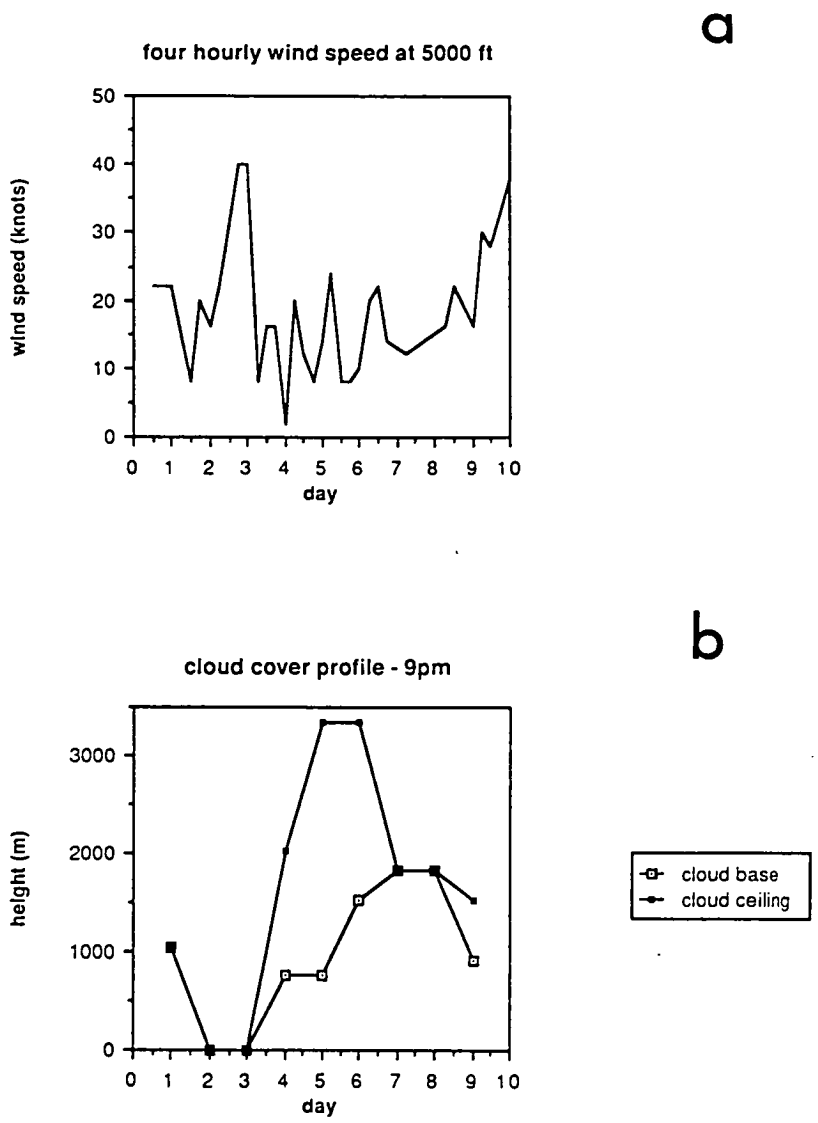


Figure 8-5.

(a) Four hourly wind speeds at 5000 feet, over Hobart from 12 - 21 January 1985.

(b) Nine pm cloud cover profile over Hobart from 12 - 21 January 1985 (open squares (□) cloud base; solid squares (■) cloud ceiling).

(c.10-12° C) compared with ambient temperature. This phenomenon has been reported elsewhere (Salisbury and Spomer 1964, Turner 1981, Fischer and Kuhn 1984). It has been suggested to be of particular importance to photosynthesis in moss cushions in the Antarctic on sunny days when cushion surface temperatures may reach 10°-15° C above ambient temperatures of 0°-5° C (Longton 1970, Seppelt and Ashton 1978).

The heavy shower activity associated with the passage of the cold front on the fourth day is clearly evident by a series of oscillations in both the air and cushion surface temperatures (depths 0.5 and 2.5 cm). More surprising are the high cushion surface temperatures reached on the subsequent days (5-7) while the mountain appeared shrouded in cloud and under the influence of light shower activity. It might be expected that under these conditions cushion surface temperatures would more closely track air temperature. However this was not the case.

It is interesting to speculate that significant photosynthesis may occur under these conditions. These weather conditions are prevalent in both alpine Tasmania and Macquarie Island. Neither the photosynthetic temperature response curve nor the photosynthetic light response curve of A. forsteroides have been determined. The temperature response curve could be expected to fall within the range of other alpine and sub-antarctic species, i.e. 10°-20° C (Greer 1984, M.J. Brown pers. comm.). However the light response curve remains a matter of conjecture although it has been suggested that alpine plants might be expected to have a high light requirement (Billings 1974b).

If, however, cushion species have a low light compensation point significant photosynthesis would be possible under cold cloudy conditions. To investigate this question it would be necessary to collect both the relevant environmental data in conjunction with short interval temperature data and to construct an infra-red gas analyzer chamber suitable for accommodating cushions. Several efforts in this direction were made but the technical difficulties proved insurmountable with the resources available. The accurate measurement of the surface area of cushion plant leaves is also likely to prove difficult.

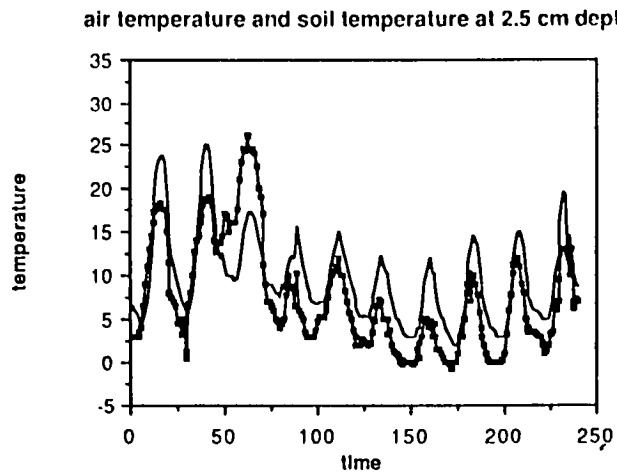
Regardless of the truth of this hypothesis the ability of cushions to attain high surface temperatures under conditions of low ambient temperature is likely to allow significant photosynthesis to occur both earlier and later in the day than

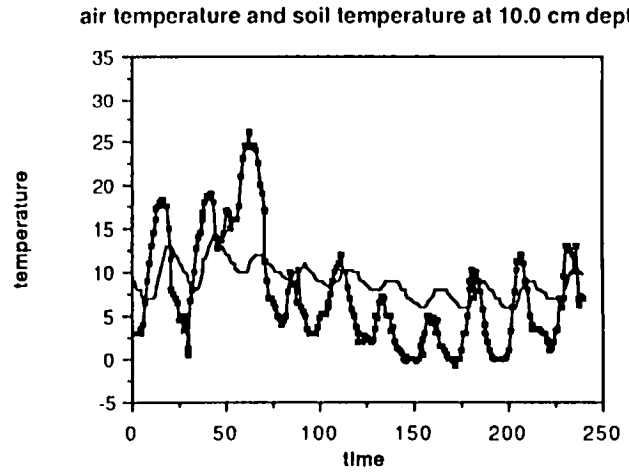
would otherwise be possible, and during calm cool days in autumn and winter. It is possible that the significant amounts of growth recorded during the 'winter' measuring period (chapter 2) were achieved by this mechanism. If this were the case it would suggest that, at least for cushion plants in alpine Tasmania, the growing season is of no fixed length and is dependent on the distribution of weather conditions suitable for this thermal warming to occur.

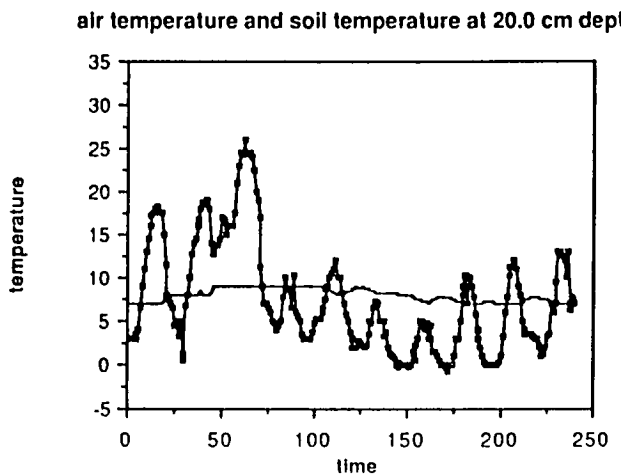
The second notable feature seen in figures 8-3 and 8-6 is the temporal shift and the dampening of temperature fluctuations in both the cushion and soil profiles. As can be seen from the first 25 hour period (figure 8-7), whilst air temperature and the temperature of the cushion at 0.5 and 2.5 cm depth peak at c. 15 hours, the temperature peak at a depth of 7.5 cm was delayed four hours and at 12.5 cm by seven hours. The soil temperatures show a similar trend but the maximum temperatures are both lower and later than those recorded for the cushion at similar depths (e.g. 2.5 cm). This observation is consistent with the data reported above showing peat soils are better thermal insulators than cushions. Finally, at the depths of 20 and 30 cm soil temperatures entirely lose a diurnal fluctuation and are responding at wavelengths in excess of 10 days (figure 8-6).This observation is in agreement with the regressions reported in chapter 2 indicating that soil temperature at 30 and 50 cm is a good estimate of the previous months mean temperature.

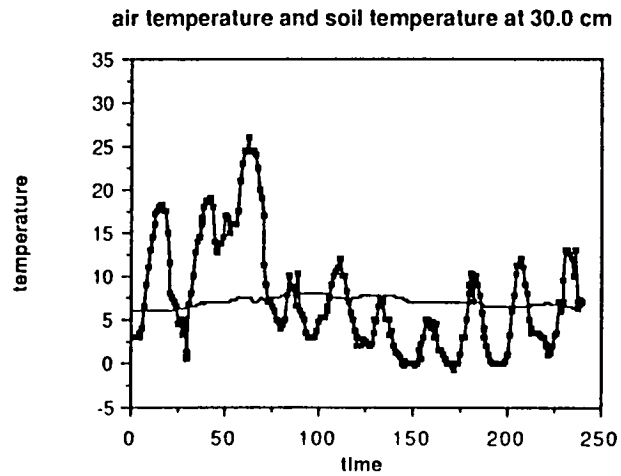
Surface cushion temperatures of the Azorella selago cushion at 370 m asl on Macquarie Island measured over a 48 hour period in December 1986 were generally within ± 2° C of ambient (figure 8-8). This reflects the prevailing weather conditions during this period which were cool and overcast with constant 15-25 knot winds with associated rain squalls and a series of three cold fronts on the second day (figure 8-4). The influence of wind in lowering the temperature differential between cushion surfaces and air has been reported by Fischer and Kuhn (1984). The close correlation between ambient and cushion surface temperature can be explained given the significant evaporative cooling of the cushion plant that could be expected under these conditions. Why this phenomenon was not found on Mt Wellington under similar conditions is not clear. The occurrence of calm and dry days could be expected to be very much lower on Macquarie Island than on Mt Wellington given its geographic location (see appendix 3). The importance to the overall carbon balance of increased photosynthesis on clear cool days is not clear. Nonetheless integrator data from the previous summer did indicate attainment of quite high surface temperatures

Figure 8-6 Air and soil temperatures at different depths between the 12 - 21 January 1985 at the Mt. Wellington site, air temperature shown by solid boxes (■) and cushion temperature by a continuous line (__).









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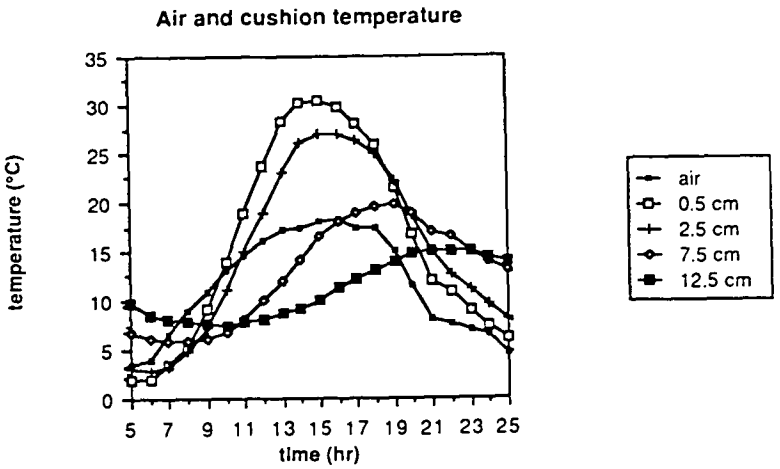

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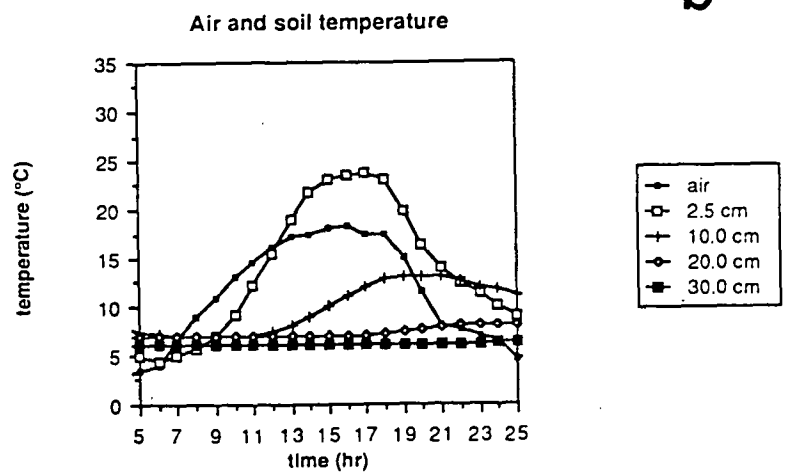
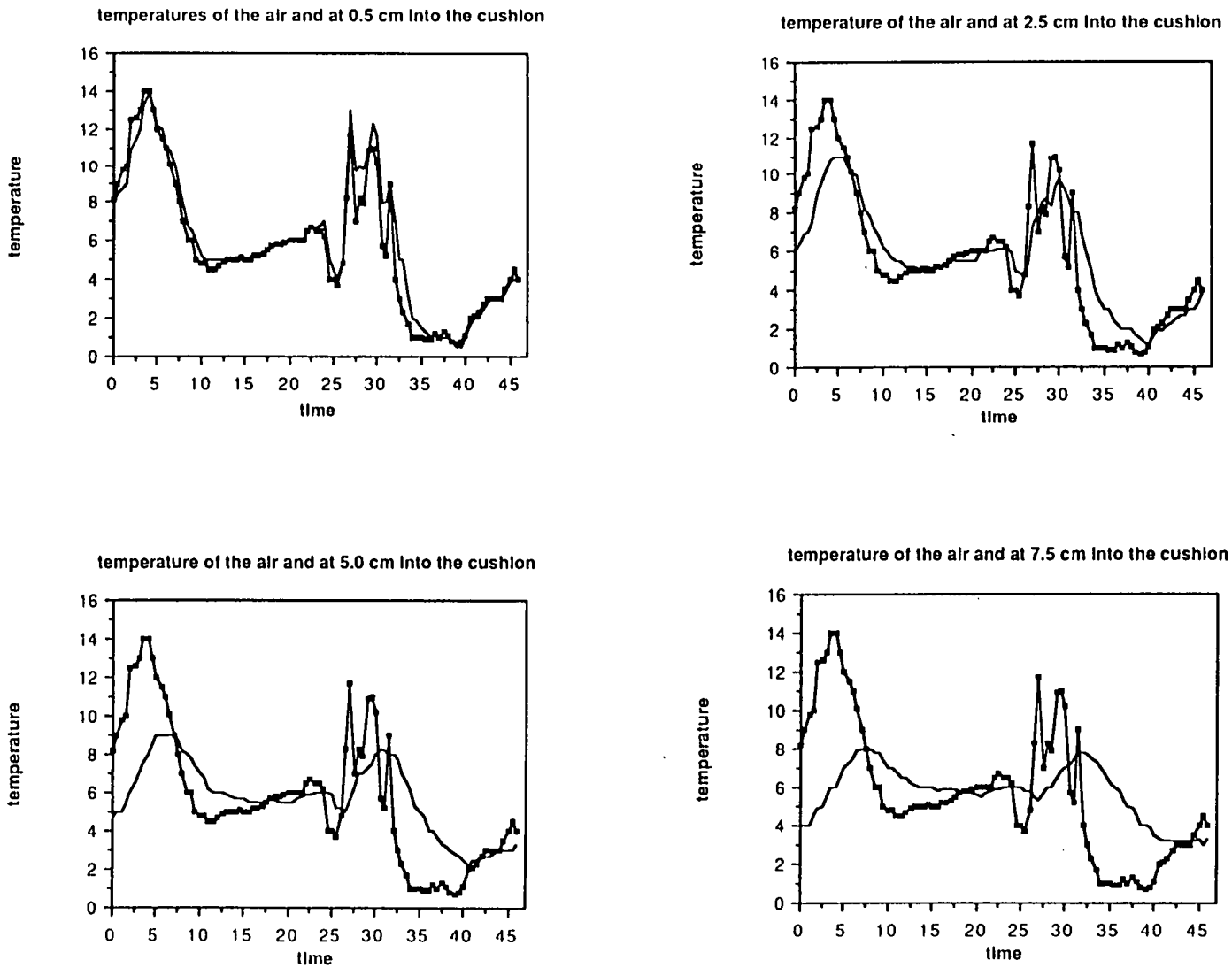


Figure 8-7

(a) Air and cushion temperatures at different depths for a 20 hour period at the Mt. Wellington site. Note the temporal shift in temperature maximums and the dampening of the fluctuations with increasing depth (depths in cm).

(b) Air and soil temperatures at different depths for a 20 hour period at the Mt. Wellington site. Likewise note the temporal shift in temperature maximums and the dampening of the fluctuations with increasing depth (depths in cm).

Figure 8-8 Air and cushion temperatures at different depths between 6-8 December 1985 at the Perseverance Bluff site on Macquarie Island, air temperature shown by solid boxes (■) and cushion temperature by a continuous line (__).



(appendix 3), and Huntley (1971) has shown the ability of Azorella selago to absorb radiation on calm days (figure 8-9).

In both the cushion and soil temperature graphs there is again an obvious dampening and temporal shifts with increasing depth (figures 8-8 and 8-10). Under the lower temperature environment of Macquarie Island there was significant lags between temperature maxima at all depths except at 20 cm depth in the soil where once again no diurnal trend was evident (figure 8-8). In the cushion this lag was a half hour at 0.5 cm, 1.5 hours at 2.5 cm, 2.5 hours at 5.0 cm and 4.5 hours at 7.5 cm. In the soil the temperature lag times were 1.5 hours at 5 cm and 4.5 hours at 10 cm (figure 8-11).

8.4 Discussion

While the cushion form appears well adapted to avoidance of root freezing due to severe subzero temperatures, in reality these temperatures are rarely if ever achieved (figure 2-4). The highly organic peat soils on which cushion plants are normally found also have even lower thermal diffusivity. While the root systems of cushion plants avoid temperature stress, the shoot systems are tolerant, capable of withstanding temperatures down to -15° C for at least short periods (table 8-3). All shoots were killed by -10° C temperatures for 40 hours (cooled from 15° C at 0.1° C/min).

Given the low thermal diffusivity of the peat soils it is likewise unlikely that temperature conditions are ever so severe that seedling death would result from root freezing. Again the situation in mineral soils was not addressed.

The ability of the cushion form to absorb significant amounts of radiation at low ambient temperatures may allow significant photosynthesis to occur during the colder months and to extend the period of photosynthesis during the summer period. The ability of cushions to absorb significant amounts of radiation was demonstrated by A. forsteroides on Mt. Wellington and can be inferred from temperature integrator data for the other Tasmanian cushion species as well as Azorella selago on Macquarie Island. It is yet to be established how significant this feature would be on Macquarie Island where high wind speeds and rain are a constant feature of the environment. How high surface temperatures were achieved by A. forsteroides under similar conditions on Mt Wellington requires further investigation. To fully assess the importance of the high surface

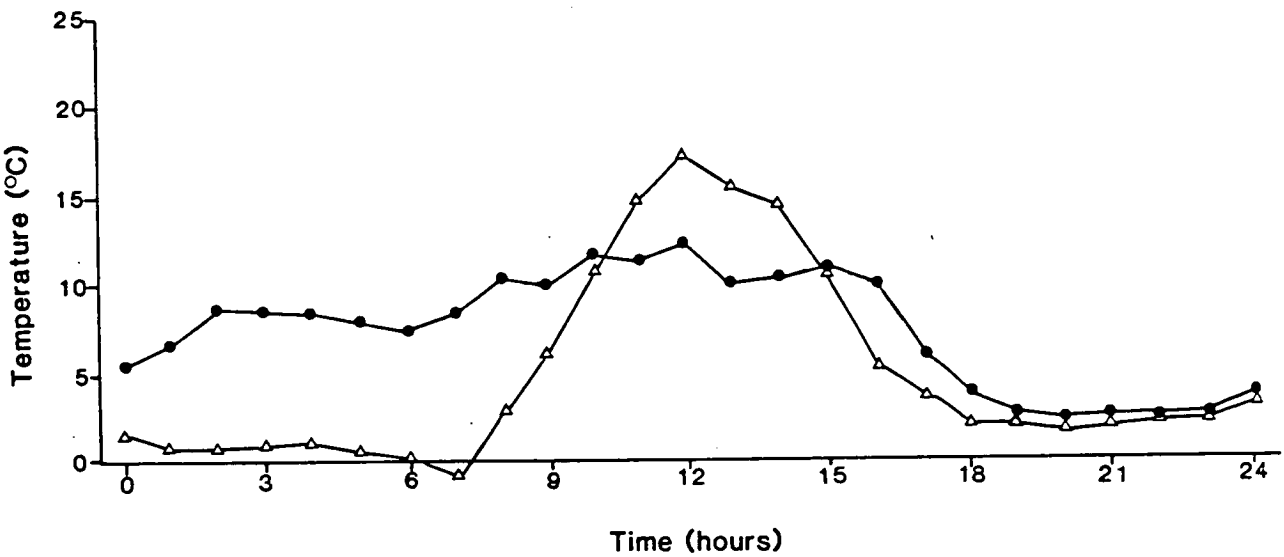


Figure 8-9 Temperature recordings from an Azorella selago fjaeldmark on Marion Island under still conditions. Air temperature, solid circles (●); cushion temperature at 2.0 cm depth, open triangles (Δ) (After Huntley 1971).

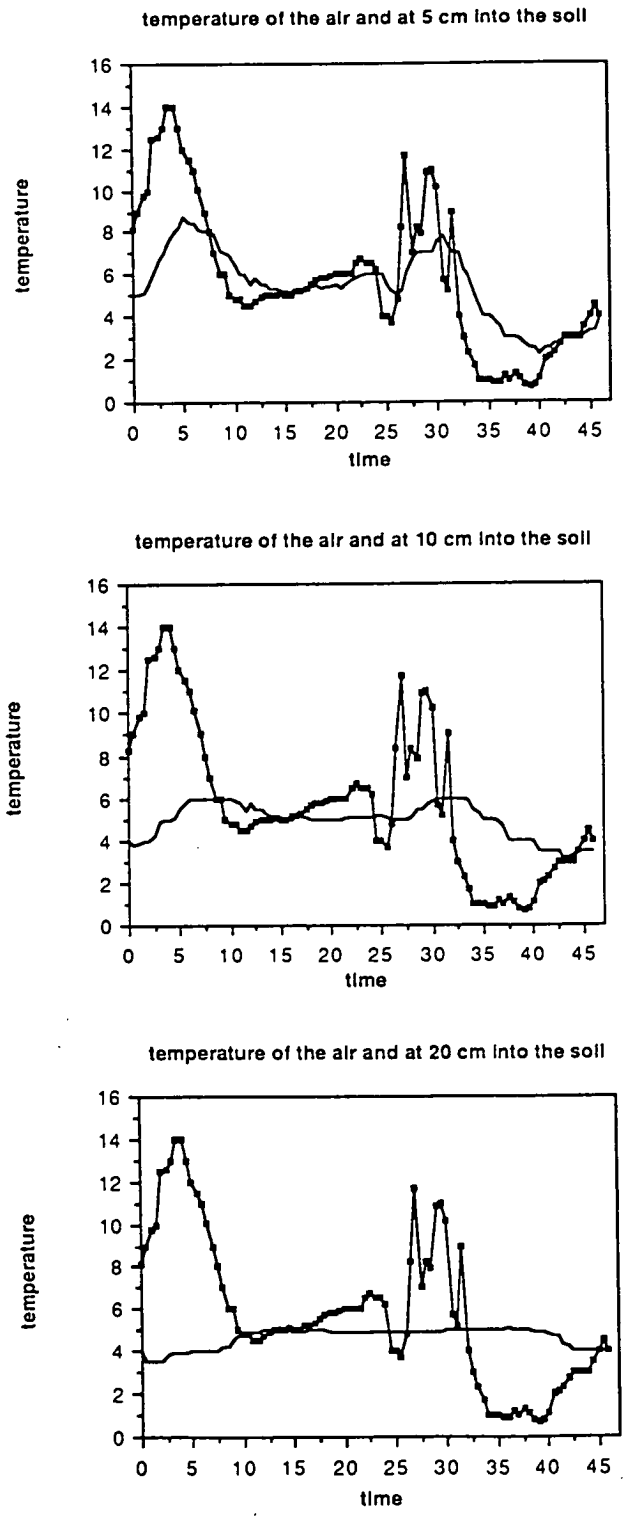


Figure 8-10 Air and soil temperatures at different depths between 6-8 December 1985 at the Perseverance Bluff site on Macquarie Island, air temperature shown by solid boxes (■) and cushion temperature by a continuous line (___).

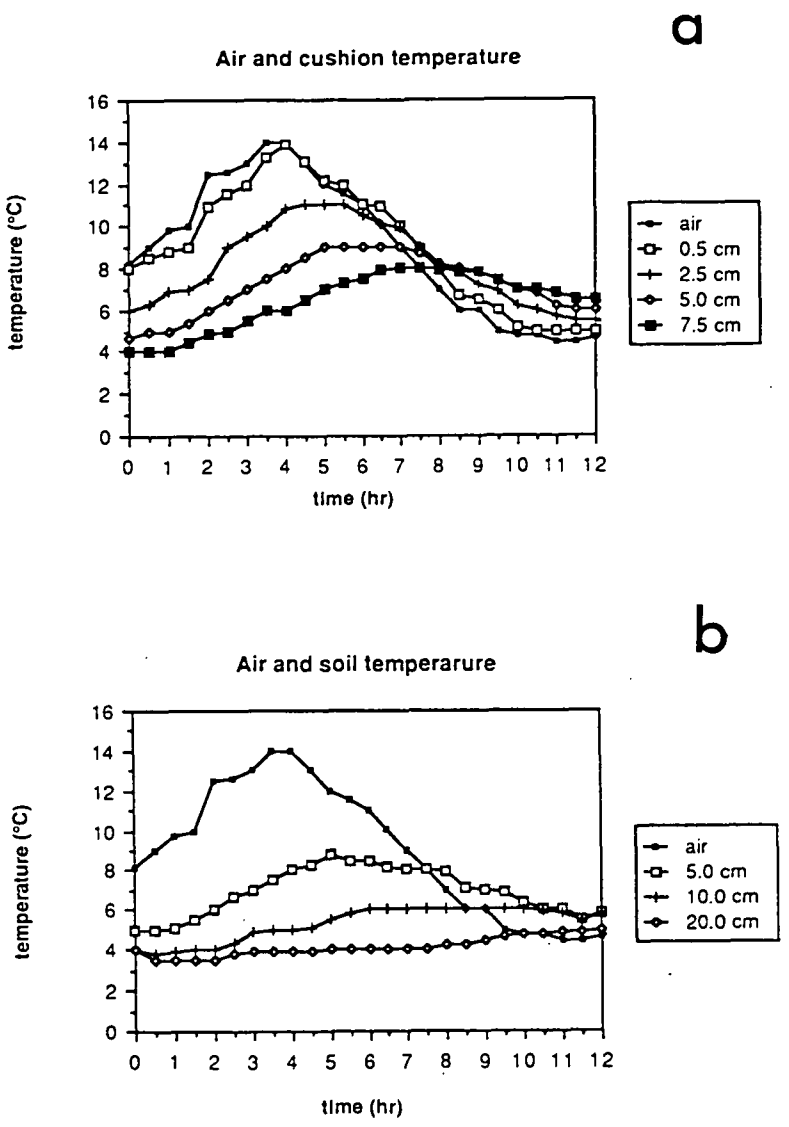


Figure 8-11

(a) Air and cushion temperatures at different depths for a 12 hour period at the Macquarie Island site. Note the temporal shift in temperature maximums and the dampening of the fluctuations with increasing depth (depths in cm).

(b) Air and soil temperatures at different depths for a 12 hour period at the Macquarie Island site. Likewise note the temporal shift in temperature maximums and the dampening of the fluctuations with increasing depth (depths in cm).

temperatures of cushions both in Tasmania and on subantarctic Macquarie Island would also require the determination of photosynthetic temperature and light response curves.

Although very high surface temperatures have been recorded in cushion plants, data from the European Alps indicate that no water stress occurs in Silene exscapa All. and Saxifraga oppositifolia L. even under conditions of high evaporative demand (Korner and de Moraes 1979). However physical drought may be experienced by cushion plants in the winter months if water uptake by the root systems is restricted by a frozen soil layer. The freezing of the surface layers of the peat soil has been recorded in the growth study (chapter 2). Given that winter water deficits are likely to occur, the anatomy of the cushion plants may need to be highly xeromorphic to survive such periods. This hypothesis is examined in the following chapter.

CHAPTER 9 INVESTIGATION OF CUSHION MORPHOLOGY AND ANATOMY

9.1 Introduction

The morphological convergence of the four species of cushion plant is marked despite their lack of taxonomic affinity (figure 9-1, 9-2). Indeed the occurrence of P. colensoi in Tasmania was not recognized until relatively recently (Curtis 1946) although a specimen was collected by Rodway in 1917. Mooney and Dunn (1970) suggested that similar lifeforms develop independently in similarly stressed geographically isolated regions because as the stresses imposed by the environment are compounded the number of biological solutions becomes increasing limited. If such an argument applies to the evolution of cushion plants in Tasmania then a high degree of anatomical convergence could be expected to parallel the morphological convergence of the Tasmanian species.

The functional role of the anatomical characters in relation to the thermal balance of cushion plants is unknown. Korner and de Moraes (1979) recorded leaf surface temperatures of 25°C, 15° C above ambient air temperature, in Silene exscapa a cushion plant from the European Alps. Despite this high leaf temperature there was no evidence of water stress. Similar results have been reported for scree plants from New Zealand where surface temperatures may rise to 40°-50° C (Fisher 1952). The availability of soil moisture and efficient transport systems appear to allow active plant growth under conditions of high to very high temperature.

During winter however high water deficits may develop if access to soil moisture is restricted by a frozen soil layer at times of high evaporative demand. (Wardle 1971, 1974; Tranquillini 1979). These conditions are likely to be prevalent at times of cold clear conditions with little or no snow (which acts as an insulating layer). Soil freezing was recorded twice during the growth study once in July 1983 and again in August 1984 (Section 2.4.1.3). These episodes of soil freezing may be more prevalent than the monthly data suggests. The severity of the water deficits of cushion plants under these conditions may be accentuated by its thermal properties, creating large temperature (and as a consequence moisture) gradients (figure 8-3). It could be expected therefore that Tasmanian cushion plants are likely to show desiccation avoidance mechanisms in order to cope with periodic winter drought (Larcher 1980).

Figure 9-1. Photographs of the surfaces of the four cushion species, (a) D. novae-zelandiae, (b) D. minimum, (c) P. colensoi, (d) A. forsteroides. (Scale bar = 10 mm)

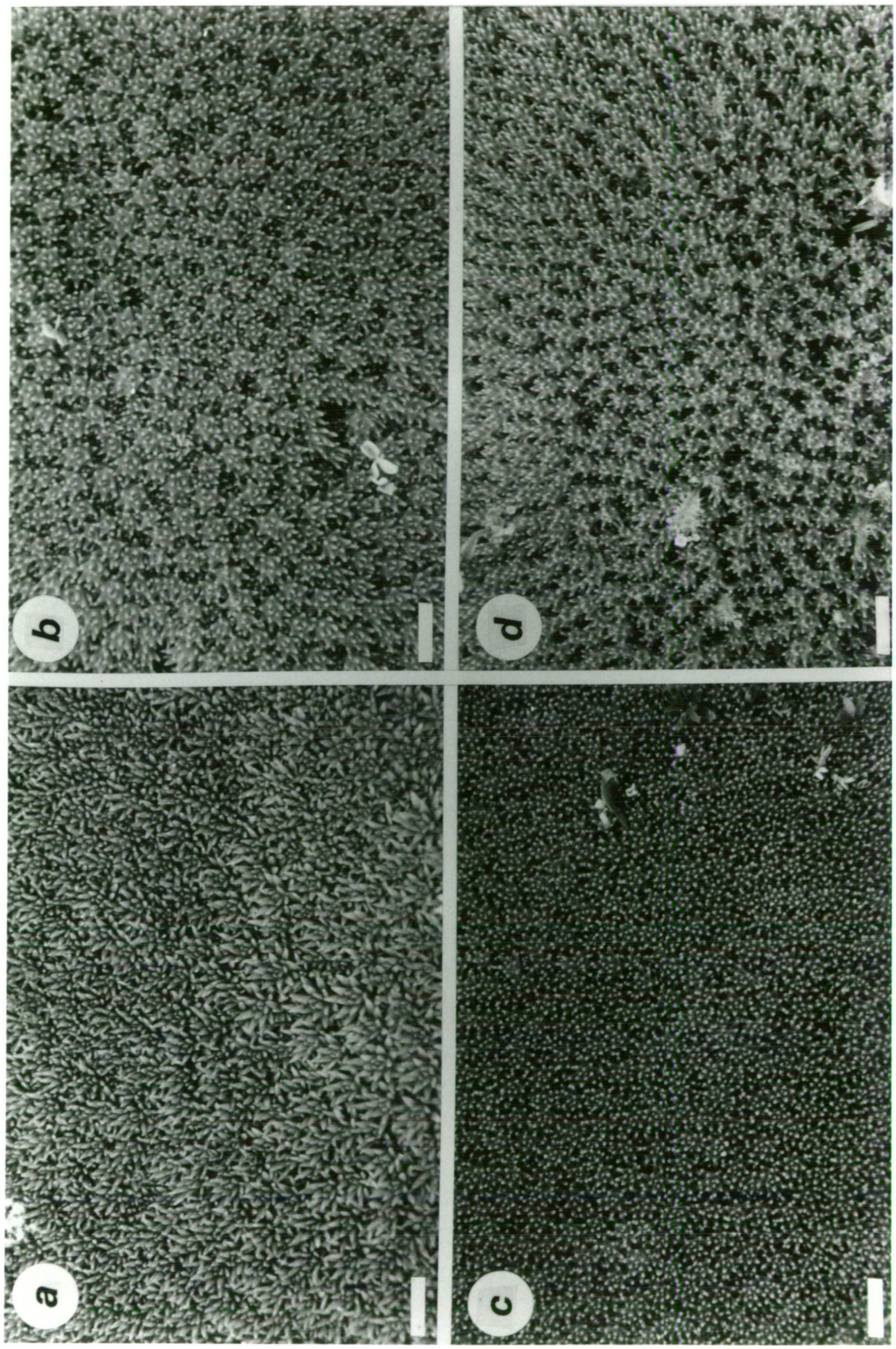
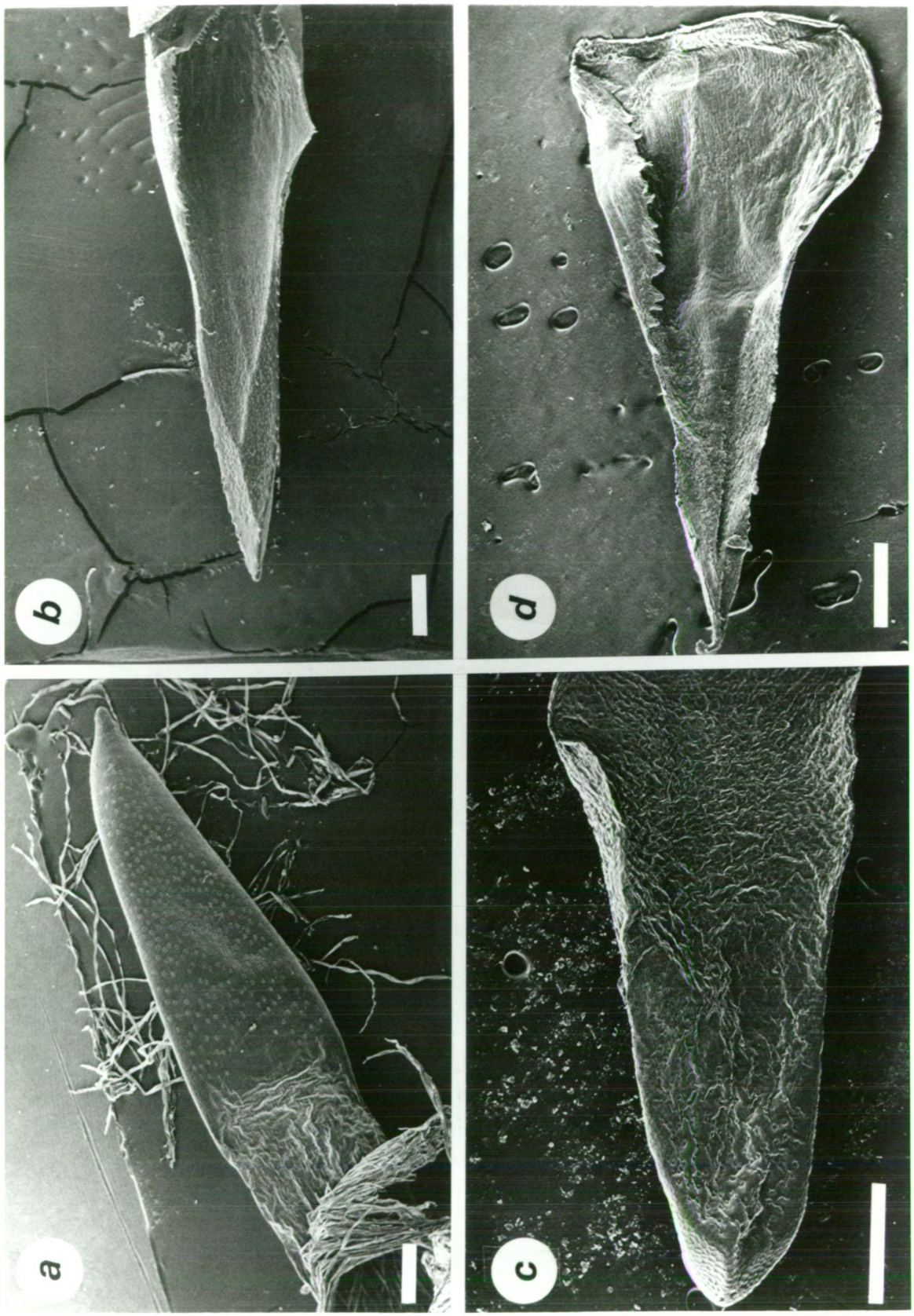

b
d
a
c

Figure 9-2. Scanning electron micrographs of the leaves of the four cushion species, (a) D. novae-zelandiae, (b) D. minimum, (c) P. colensoi, (d) A. forsteroides. (Scale bar = 0.5 mm).


b
d
a
c

This chapter describes a study of cushion plant anatomy undertaken to test the hypotheses that:

(a) a high degree of anatomical convergence is likely to be exhibited by the four cushion plant species, and

(b) the anatomy of the leaves of the cushion plants are highly xeromorphic.

9.2 Methods

Fresh and preserved material from the four cushion plant species was collected from Mt. Field West and Mt. Wellington. Both wax and freezing microtome sectioning were used to obtain 10-15 µm transverse (TS) and longitudinal sections (LS) of the leaves and stems of the cushion plants. Sections were stained with safranin and fast green or toluene blue. Leaf sections were obtained from a range of locations along the lamina, while stem sections were taken about 1 cm below the shoot apex. Anatomical diagrams were drawn using a camera lucida.

Cuticles were also prepared by clearing the leaf in a nitric acid and potassium chlorate solution and neutralizing it in aqueous ammonia. The cuticle was then split using fine forceps, stained with safranin and mounted. Scanning electron micrographs of the leaves and leaf surfaces were obtained from fresh material.

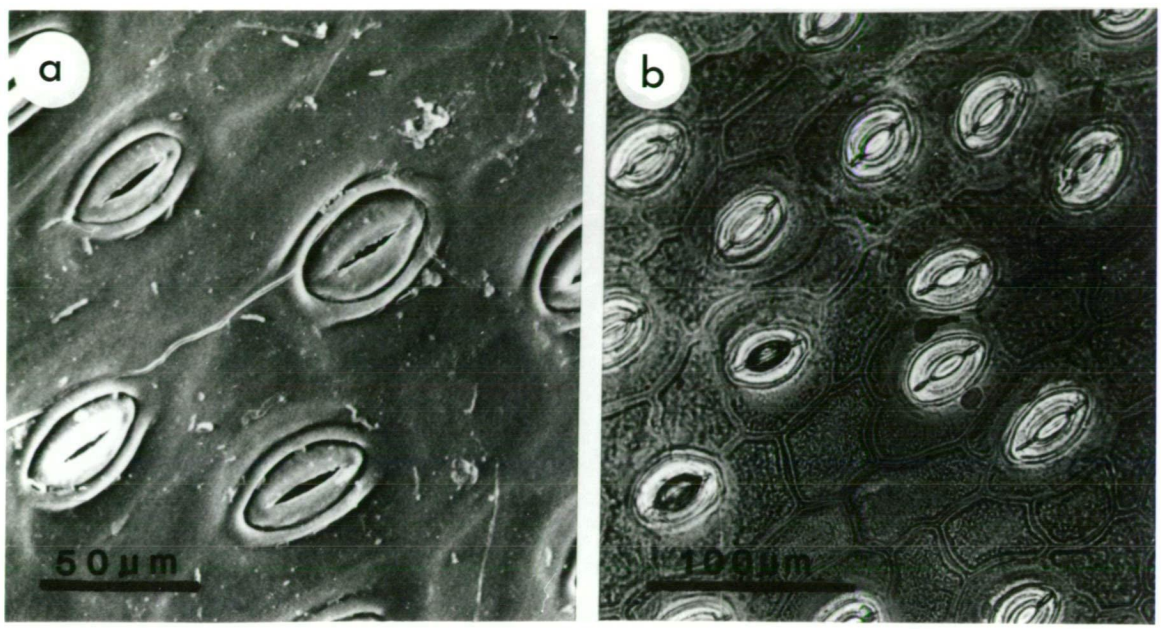
9.3 Results

Although gross morphology and structural organization of all four species are very similar leaf morphology and anatomy are much more variable.

9.3.1 Donatia novae-zelandiae

Leaf morphology: Leaves are sessile 5-6 mm long linear-subulate with a pointed apex. The leaf base is widened and has dense tufts of white hairs 2-3 mm in length in the leaf axis (Curtis 1963). Stomata are apparent on both surfaces with the guard cells being surrounded by a distinctive cuticular ridge (figures 9-2a, 9-3a).

Figure 9-3. Cuticle of D. novae-zelandiae shown by (a) SEM and (b) light microscope. (After Gibson et al. 1987).


a
50µm
b
100µm

Anatomy

Leaf surface: Stomata are 40 µm long and 30 µm wide. All stomata are arranged parallel to the long axis of the leaf (figures 9-2a, 9-3a & b). Epidermal cells are variable in shape but have distinct cell wall thickening. The leaf cuticle is an extremely inert substance which has proved useful in identifying 20,000 year old cushion plant fossils (Gibson et al. 1987).

Leaf TS: A single layer of epidermal cells is covered by a thick cuticle (figure 9-4b). No palisade mesophyll is present. Spongy mesophyll with numerous chloroplasts is traversed by 3 (-5) vascular bundles. The central vascular bundle is bound by a bundle sheath and is comprised of xylem and phloem and a large cap of sclerenchyma. The minor vessels are similar though without a bundle sheath (figure 9-4a). Toward the base of the leaf up to 5 vessels are present.

The stomata occur regularly over both leaf surfaces. The distinct cuticular ridge surrounding each stomate is formed by small outgrowths of the guard cells which effectively limit the extent of the cuticle (figure 9-4b). The guard cells also have ledges into the stomata on both upper and lower surfaces. Beneath the stomata spongy mesophyll and large air spaces are found (figure 9-4b). There are no surface trichomes.

Stem TS: The stem of D. novae-zelandiae is simple. There is an epidermis surrounding a thick cortex layer (figure 9-4c) with a single vascular bundle surrounded by a bundle sheath. Stem diameter is approximately 2 mm.

9.3.2 Dracophyllum minimum

Leaf morphology: Leaves are sessile with a broad sheathing base about as long as the blade (3-4 mm), narrow - lanceolate and slightly concave, thick and rigid. The apex is acute with leaf margins minutely serrate (Curtis 1963). The stomata are very small and occur on both surfaces (figures 9-2b, 9-5a).

Anatomy

Leaf surface: The stomata are c.15 µm in length and arranged parallel with the long axis of the leaf (figure 9-2b, 9-5a,b). The epidermal cells are much

Figure 9-4. Anatomy of D. novae-zelandiae (a) leaf T.S., (b) stomate, (c) stem T.S.

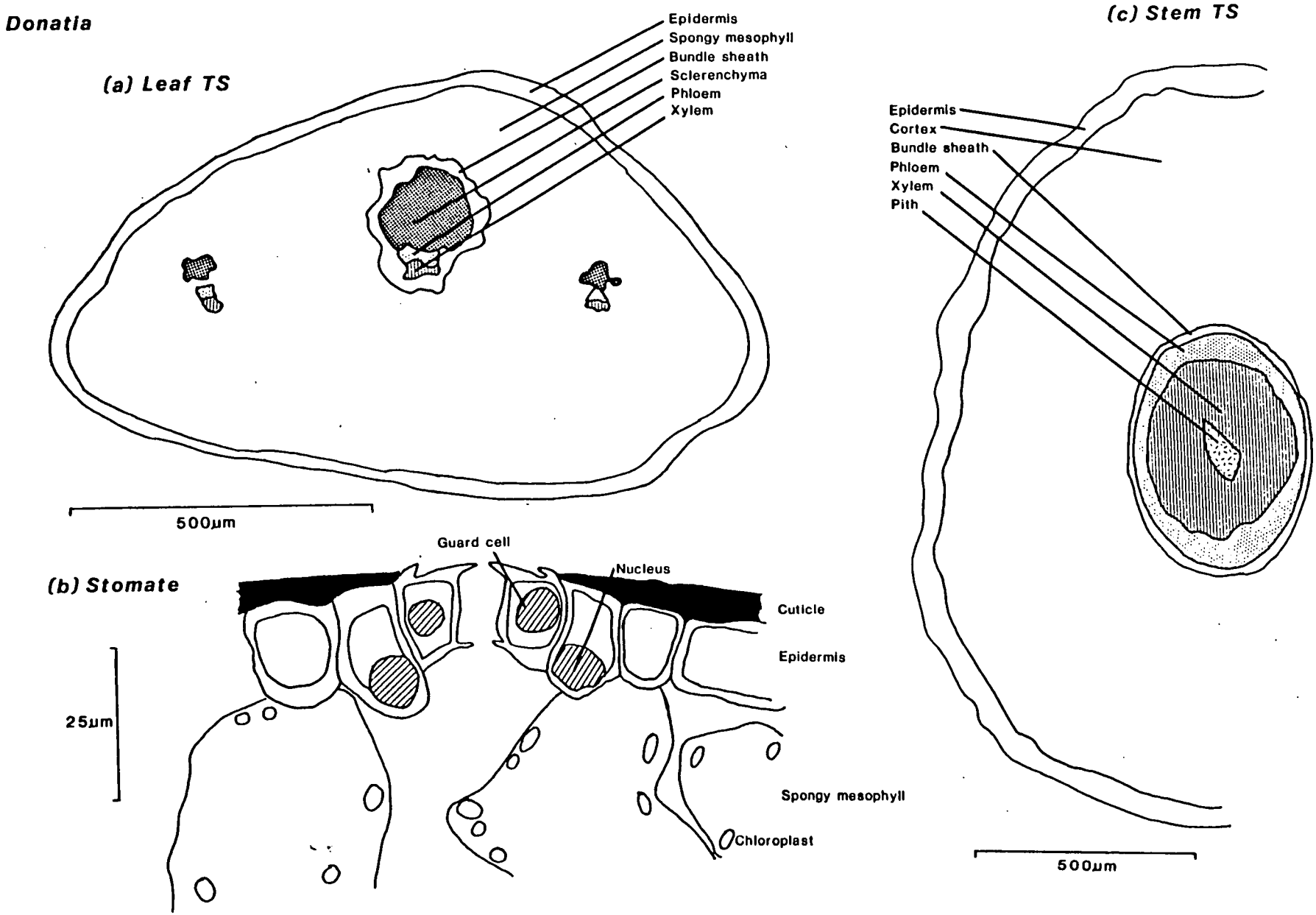
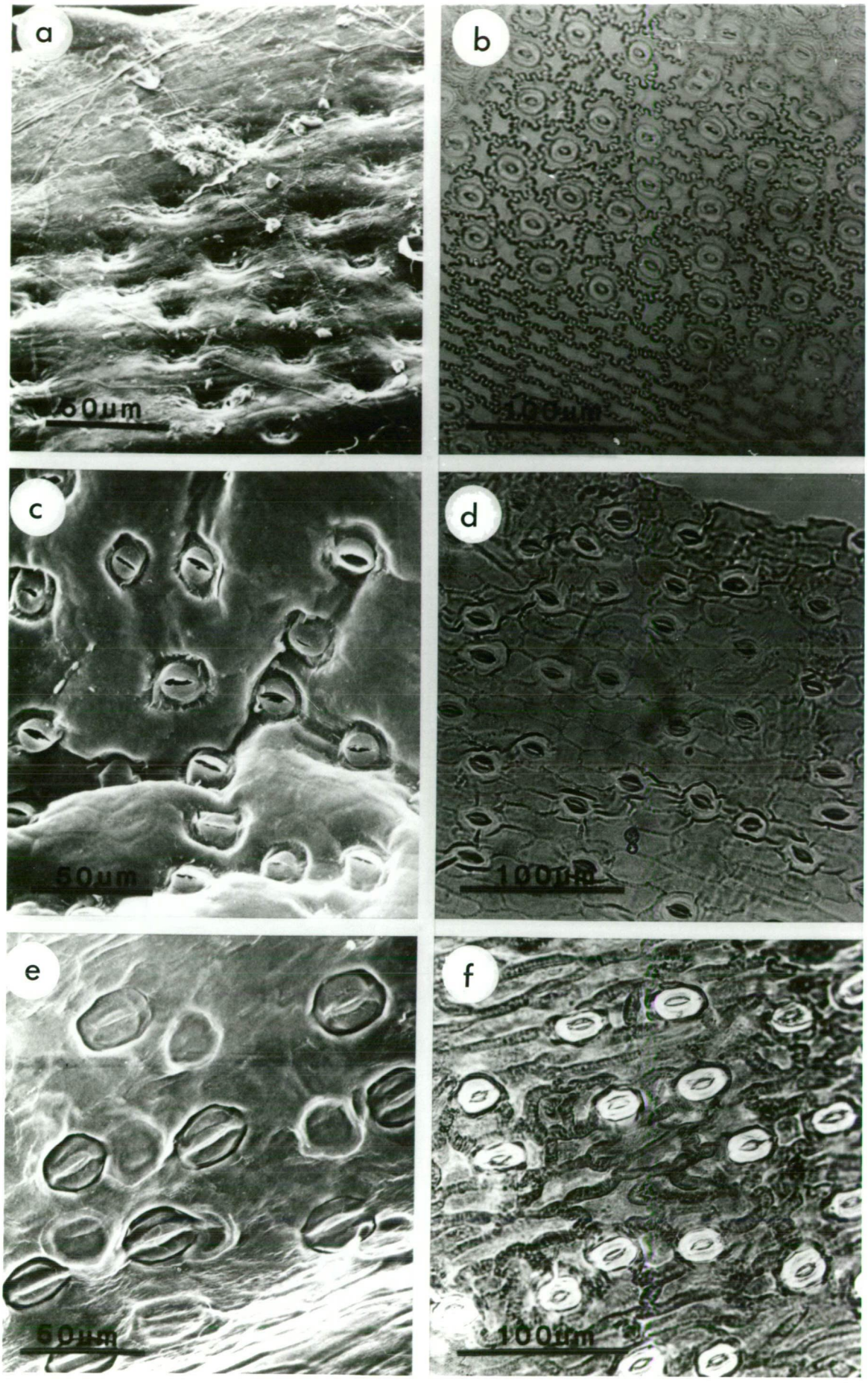


Figure 9-5. Cuticle of bolster species shown by both SEM and light microscope, (a,b) D. minimum, (c,d) P. colensoi, (e,f) A. forsteroides. (After Gibson et al. 1987).


a
50µm
b
100µm
c
50µm
d
100µm
e
50µm
f
100µm

smaller than those of D. novae-zelandiae and have highly sinuous walls. No trichomes are present.

Leaf TS: A thin cuticle covers a single layer of epidermal cells. A single layer of palisade mesophyll surrounds an inner core of spongy mesophyll through which 5 (-9) vascular bundles pass (figure 9-6a). The main vascular bundle is again capped by a large bundle of sclerenchyma. Two minor veins are also sclereid capped while the remaining veins are usually not. Phloem in all ~~vessels~~ veins appears centrally. In the broad sheathing leaf base up to 9 veins are present. The stomata occur regularly over both leaf surfaces and are very slightly sunken. The stomata consist of a pair of small guard cells, each situated above a subsidiary cell, both having a cuticular covering. The stomata are very simple with no ledges (figure 9-6b).

Stem TS: The stem of young D. minimum is very similar to D. novae-zelandiae except that the pith is more developed, often containing holes. A single epidermal layer encloses a cortex and a single vascular bundle. Stem diameter is approximately 1 mm (figure 9-6c).

9.3.3 Phyllachne colensoi

Leaf morphology: Leaves sessile, 3-4 mm long glabrous, the lower half widened and flattened, the upper half linear and thick with a glandular pore just below the apex on the adaxial side (Curtis 1963). Stomata approximately 25 µm in length occur on both surfaces (figures 9-2c, 9-5c). The leaves are often olive green in colour.

Anatomy

Leaf surface: The stomata are considerably larger than those of D. minimum (25 µm cf. 15 um). Epidermal cells are 30 µm in length and have relatively thin cell walls. No trichomes are present (figures 9-5c, d).

Leaf TS: The leaf of P. colensoi is very simple. It is composed of a moderately thick cuticle over a single epidermal layer of cells. This surrounds a core of spongy mesophyll which contains three vascular bundles each surrounded by a bundle sheath (figure 9-7a). There is no sclerenchyma in the leaf. The main vascular bundle is only slightly larger than the subsidiary veins.

Figure 9-6. Anatomy of D. minimum (a) leaf T.S., (b) stomate, (c) stem T.S.

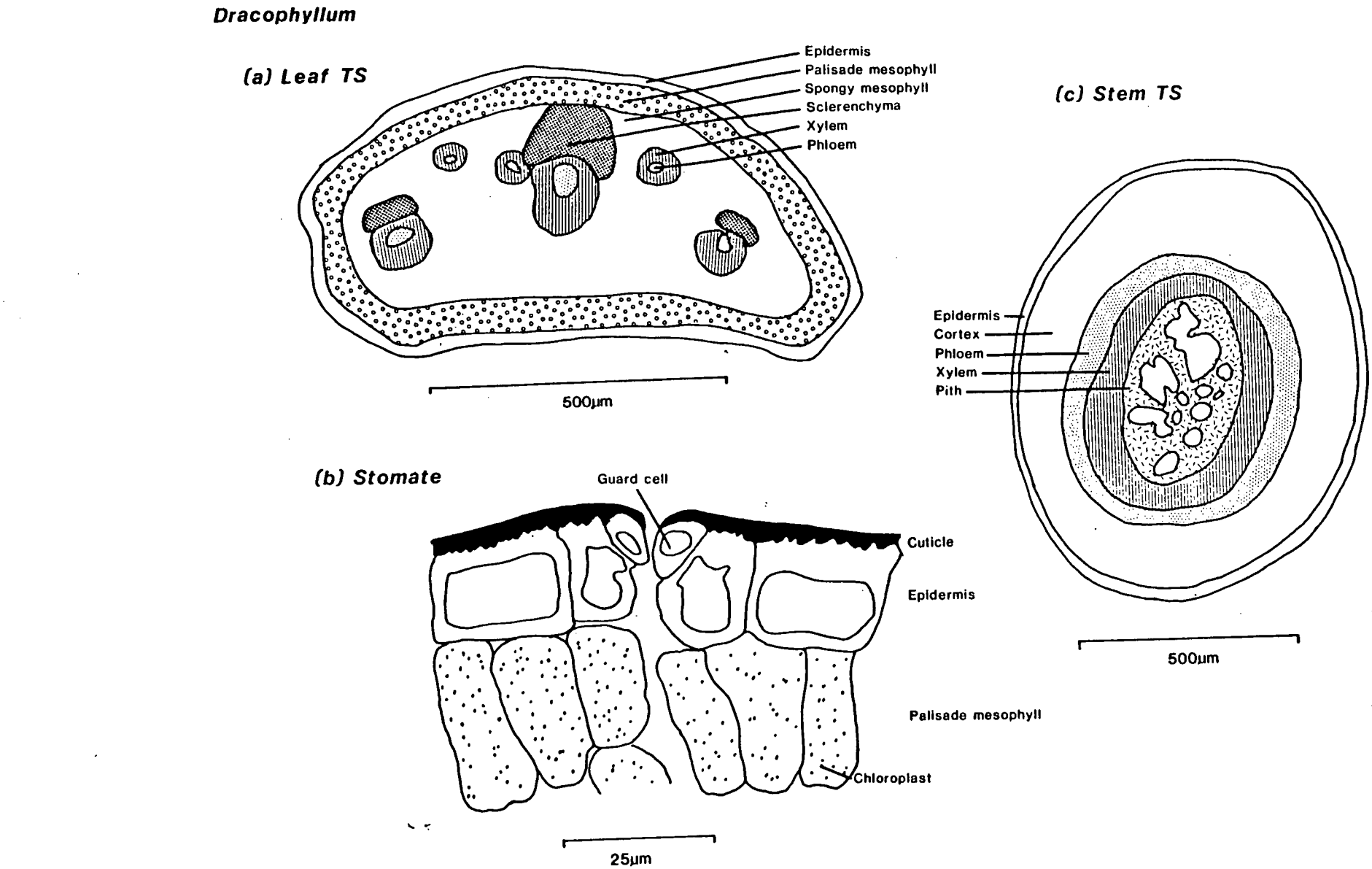
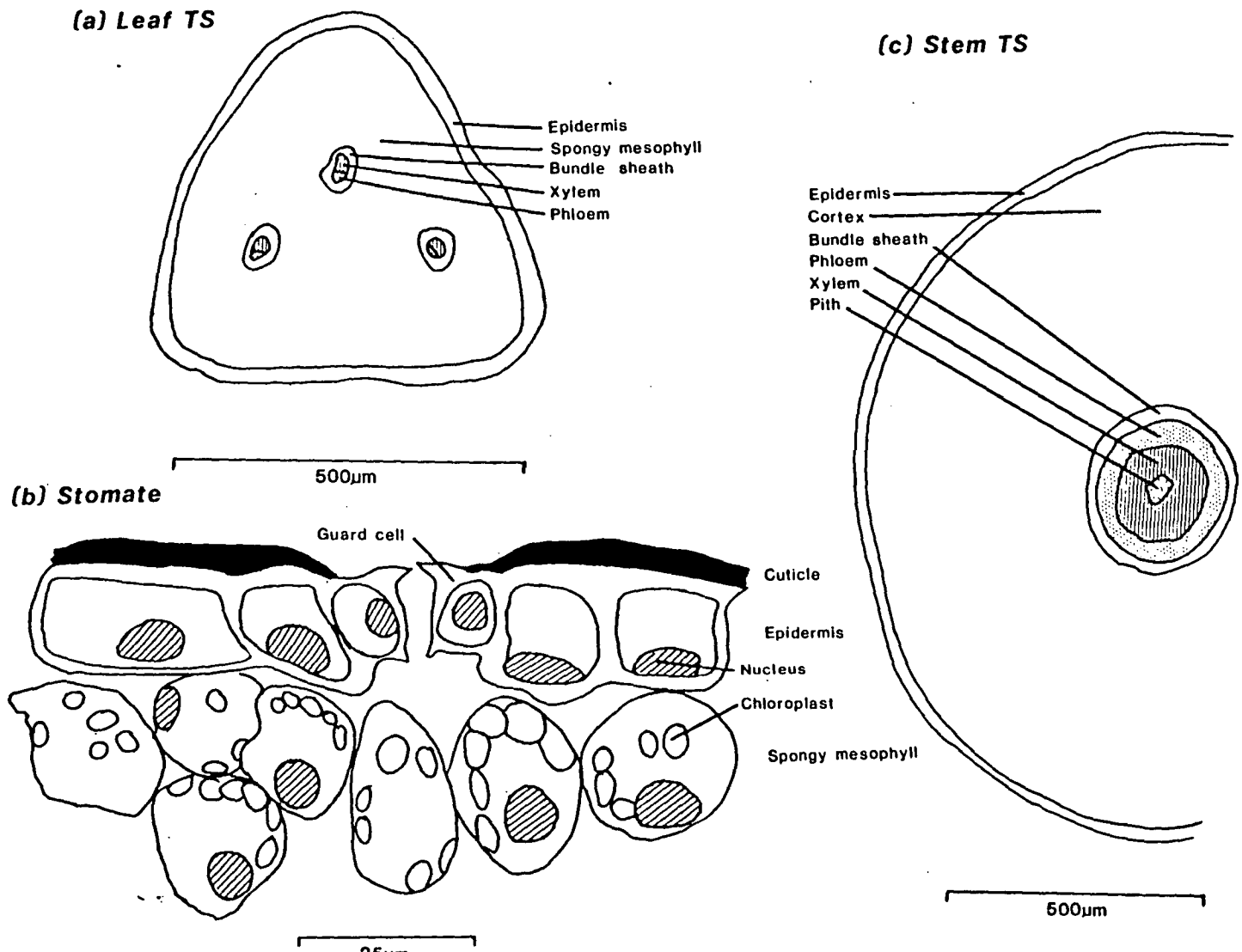


Figure 9-7. Anatomy of P. colensoi (a) leaf T.S., (b) stomate, (c) stem T.S.

Phyllachne



The stomata occur regularly over all surfaces. The guard cells are covered by a thin layer of cuticle and raised guard cells have both upper and lower ledges above a substantial space. The guard cells are surrounded by a slightly modified ~~companion~~ subsidiary cell (figure 9-7b).

Stem TS: The stem of P. colensoi is very similar to the related D. novae-zelandiae with an outer cortex layer and a single central vascular bundle with a central pith (figure 9-7c). Although D. novae-zelandiae is placed in its own monogeneric family (the Donatiaceae) by most authors due to incomplete fusion of the style and stamens, earlier work had placed it in the Stylidiaceae (see Curtis 1963).

9.3.4 Abrotanella forsteroides

Leaf morphology: Leaves are sessile c. 4 mm long with a broad sheathing base. The leaf tip is hyaline and acuminate, the leaf margins are obscurely blunt and serrulate (Curtis 1963, Gibson et al. 1987) (figure 9-2d). The hyaline leaf tip can give the otherwise green cushion a silvery appearance when a hand or finger is run across the cushion surface. Stomata occur in bands up both surfaces (figure 9-5e).

Leaf TS: The single layer of epidermal cells is covered by a thick layer of cuticle (figure 9-8a). Sunken multicellular trichomes are scattered over the leaf surface (figure 9-8b). These structures are made of 10-15 cells, are broadly cuneate and are attached to the leaf surface by a modified epidermal cell. The trichome tip is slightly sunken below the leaf surface and is c. 30 µm in length and c. 25 µm broad at the top. Within the trichome cavity cuticle thickness becomes attenuated, so that the trichomes are almost completely free of cuticle.

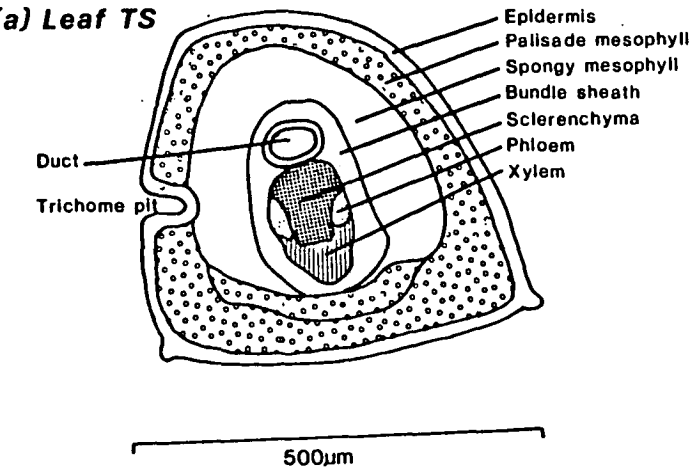
There are two layers of palisade mesophyll on the adaxial surface but only one on the abaxial surface, a layer of spongy mesophyll traversed by a single vascular bundle. The bundle is enclosed in a sheath and includes a major duct, a sclereid cap, phloem and xylem tissues (figure 9-8a,c).

The duct appears empty and is surrounded by a distinct epidermis. It is c. 100 µm in diameter and LS sections show it to run the full length of the leaf. Its function remains obscure.

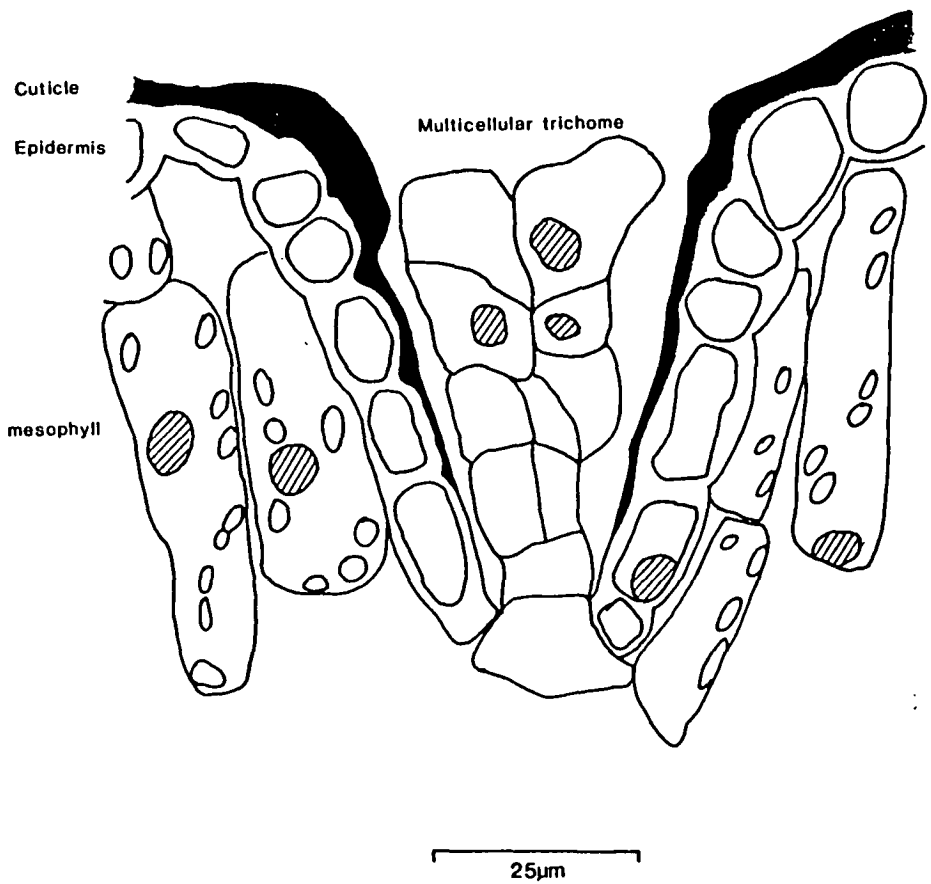
Figure 9-8. Anatomy of A. forsteroides.(a) leaf T.S., (b) trichome, (c) vascular bundle, (d) stomate, (e) stem T.S.

Abrotanella

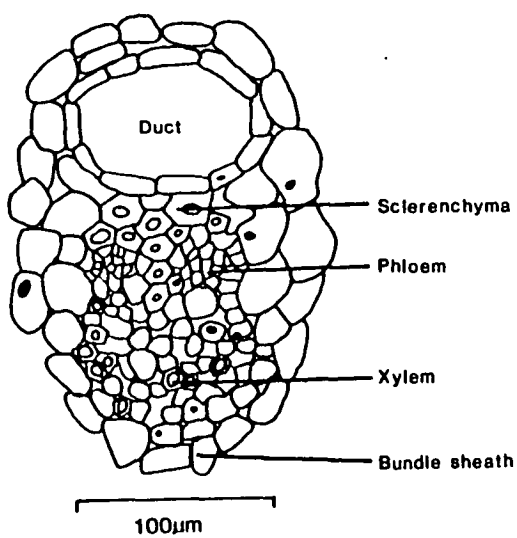
(a) Leaf TS

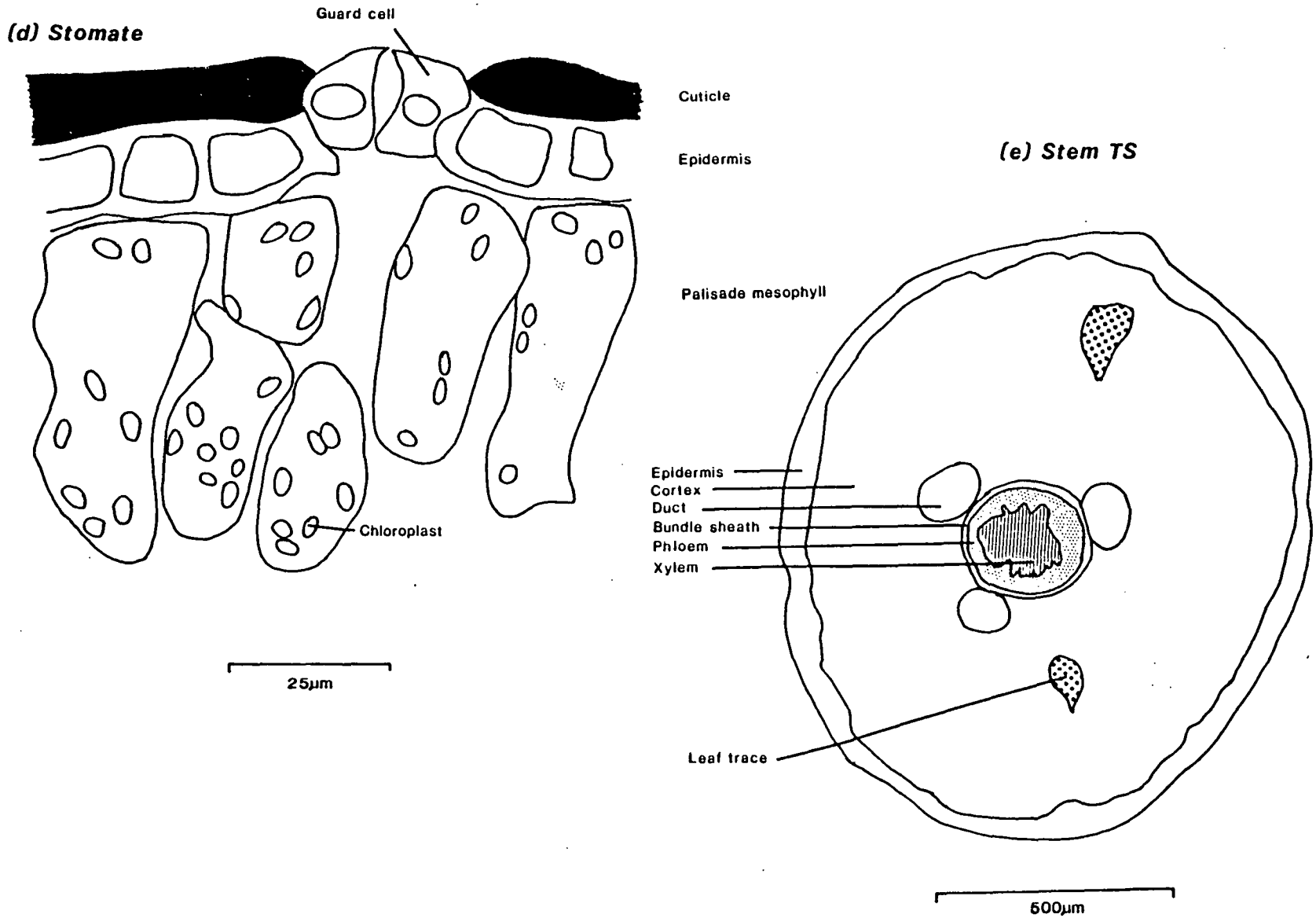


(b) Multicellular trichome



(c) Vascular bundle




(d) Stomate
Guard cell
Cuticle
Epidermis
Chloroplast
25µm
(e) Stem TS
Palisade mesophyll
Epidermis
Cortex
Duct
Bundle sheath
Phloem
Xylem
Leaf trace
500µm

The phloem tissue is split into two discrete bundles by an intrusion of sclerenchyma in the lower half of the leaf.

The stomata appear on both leaf surfaces in broad bands running parallel to the leaf axis (figures 9-5e,f, 9-8d). The stomata are c. 30 µm in diameter and very simple with no ledges or ornamentation. The leaf cuticle does not cover the guard cells (figure 9-8d).

Stem TS: The stem in TS is similar to the other three species except for the inclusion of three major ducts (figure 9-8e) A two layer epidermis encloses a cortex and the single vascular bundle is enclosed by a sheath. Immediately outside this sheath are three ducts identical in form to that found in the leaf. Stem diameter is c. 1 mm whilst the ducts are c. 100 µm in diameter.

9.4 Discussion

All four species of cushion plant show a high degree of morphological convergence. All have closely compacted, highly branched stems with very short internodes between the leaves. All the leaves are sessile, small and ridged with stomata on both surfaces.

The internal structure is much less uniform and consequently more difficult to compare. Of the four species D. novae-zelandiae and P. colensoi are the most similar. The major differences between the two species are the lack of sclereids in P. colensoi. Nonetheless the internal structure and stomata are very similar (figures 9-4, 9-7). This similarity is not surprising given the taxonomic affinity between these species (see Curtis 1963).

D. minimum has a quite distinct anatomy with a palisade mesophyll and numerous minor veins all running parallel with the leaf axis. Its internal structure is almost identical to the closely related New Zealand cushion plant Dracophyllum muscoides except for the absence of the second palisade layer on the adaxial surface (Hauri 1916).

A. forsteroides shows the most complex anatomy, with the presence of well developed ducts through leaves and stem, and the presence of sunken multicellular trichomes (figure 9-8). The function of both these structures is

obscure, but the ducts may be important in the aeration of plants growing in highly anaerobic peats.

It is difficult to quantify the degree of dissimilarity between the four cushion species because no comparative data is available for other life forms found in this environment and the functional significance of many anatomical features are poorly understood (e.g. ducts in A. forsteroides). As a consequence the testing of the validity of Mooney and Dunn's theory of restricted biological solutions must await further data collection.

All species show xeromorphic characters but the degree of expression differs. Early in this century possession of such characters was considered to be an adaptation to water stress. However since that time it has been recognized that many mesophytes possess xeromorphic characteristics (Seddon 1974). Table 9-1 shows the typical xeromorphic characteristics, possessed by the four cushion species, generally equated with severe water stress (Jeffrey 1987). It can be seen that although all species do exhibit some xeromorphic characters none, except perhaps for A. forsteroides, could be considered to be particularly well adapted to cope with the severe water stress that might develop under conditions of restricted soil moisture and high ambient temperature. From these anatomical studies it would appear that cushion plants would primarily cope with periods of high evaporative demand by stomatal closure, since the common features shared by the four species are a thick epidermis and cuticle. The lack of sunken stomata and protective trichomes suggest such periods of stress are relatively short lived.

Both A. forsteroides and D. minimum have a well developed palisade layer, and well developed vascular bundles in their leaves (3-5-7 bundles/leaf in the case of D. minimum and a large central xylem vessel in the case of A. forsteroides). Considerably less well developed bundles are present in the other two species, however these species lack a tightly packed palisade layer. These features are consistent with all four species having efficient water uptake mechanisms capable of dealing with periods of high temperature during summer when an excess of soil water is available. The detailed study of water use patterns by bolster species is clearly needed to fully understand both the anatomical variability and the patterns of dry matter production of these species. Time constraints limited research in this direction.

Table 9-1 Xeromorphic characters often asscciated with adaptation to water stress by cushion species (after Jeffrey 1987).

	Donatia	Dracophyllum	Phyllachne	Abrotanella
Microphyllous habit	+	+	+	+
Thick epidermis	+	+	+	+
Abundant sclerenchyma	+	+	-	+
Thick cuticle	+	+	+	+
Tightly packed mesophyll	-	+	-	+
Sunken stomata	-	-	-	-
Numerous protective trichomes	-	-	-	-

Sclerenchyma is absent from the leaves of P. colensoi despite the occurrence of this species on some of the driest sites on which cushions plants occur in Tasmania (e.g. the dolerite block fields on Mt. Field West). This suggests that the presence of sclerenchyma may not necessarily be correlated with resistance to moisture stress (cf. Jeffrey 1987). Beadle (1966, 1968) has suggested that xeromorphs are extremely resistant to mineral starvation. He argued that where phosphorus and nitrogen are limiting, excess carbohydrate produced by photosynthesis is converted into cell wall material (eg.lignin in sclereids). This explanation may also apply to cushion plants. The highly acid, often waterlogged peats in which the cushion plants grow can be expected to be very low in available phosphorous and nitrogen (see Chapter 2, Swift et al. 1979). It is interesting to note that P. colensoi which is generally considered to grow on the best drained sites (Kirkpatrick et al. 1985) and sometimes on mineral soils, shows no development of sclerenchyma. The same species occurs in bogs in New Zealand and a comparative study of material from those sites might be illuminating.

Armstrong (1975) considers that the xeromorphic nature of many wetland plants is a mechanism to reduce the velocity of water flow on the anaerobic conditions at the root surface, so as to allow sufficient time for the oxidation of phytotoxins. It is tempting in the case of A. forsteroides to suggest the leaf and stem ducts might be implicated in the oxygenation of root systems.

Both the nutrient starvation and the oxygenation hypothesis could be tested for the four cushion species in glasshouse trials, however given the slow growth rates of these species these experiments would require a considerable period of time.

It appears that the internal structure of the four Tasmanian cushion plant species have not undergone significant convergence (except perhaps for the closely related D. novae-zelandiae and P. colensoi) although this is difficult to quantify. It is interesting to note that other studies of the comparative anatomy of cushion plants have report a similar degree of variability (Ancibor 1971, 1980, 1981). In a study of 14 species from the cold arid puna region of Argentina (rainfall c. 300 mm; altitudes 3400-5100 m) where high levels of water stress might be expected, it was found that most of the anatomical features could be interpreted in terms of minimization of the effects of strong

radiation, low temperatures and wind rather than a response to water deficits (Ancibor 1980).

It appears that while the particular environments may preferentially facilitate the evolution of the cushion form, the selective pressures for this may be acting at the morphological rather than the anatomical level.

All four Tasmanian species show some development of xeromorphic characters. However these are not consistent with the hypothesis that these species would undergo significant periods of winter desiccation. Rather some features such as reduced leaves and well developed cuticle are likely to be either genetic/phenotypic adaptation to extreme environmental parameters (e.g. ice ablation, high winds) while other features may be adaptations related to mineral starvation or waterlogged conditions. The extent to which these anatomical features are genetically fixed is unclear.

CHAPTER 10 GENERAL DISCUSSION AND CONCLUSIONS

10.1 Factors controlling cushion plant distribution in Tasmania

In Tasmania the controlling influences on the alpine vegetation in general are a south west - north east gradient related to fertility, altitude and soil drainage conditions (Kirkpatrick 1982, Kirkpatrick and Brown 1984, Kirkpatrick et al. 1985). Snow lie plays little role in determining vegetation patterns except in very localized areas (Gibson and Kirkpatrick 1985b). This results from the low relief and maritime climate of Tasmania compared with the continental and high alpine zones of the northern hemisphere, South America and New Zealand. Indeed snowfall while occurring at all times of the year is usually an ephemeral event. This is reflected by the shrubby nature of much of the alpine vegetation in Tasmania compared with the grass and herb dominated vegetation of the other alpine regions (Billings and Mooney 1968). Tasmania completely lacks the high alpine zone of New Zealand and has only 10 obligate alpine species out of a flora of some 300 species (Kirkpatrick 1986). The subdued relief and lack of a high alpine zone was considered to be the major reason for the high degree of intergradation seen in the Tasmanian cushion plant communities when compared to the highly distinct South Island cushion communities sampled by Gibson and Kirkpatrick (1985a). This was presumed to result from much steeper and more extended environmental gradients being apparent in New Zealand as well as reflecting a more complicated geology.

One of the three main aims of this thesis was to investigate the ecological differentiation of four bolster species (A. forsteroides, D. novae-zelandiae, D.minimum and P. colensoi). The distribution patterns of these species have been presumed to be at least partially under the control of the SW-NE fertility gradient, altitude and soil drainage (Kirkpatrick 1982, 1983; Kirkpatrick et al. 1985), however none of these hypothesis had been tested experimentally. Consequently a series of more refined hypothesis (listed below) were set up to test these ideas using data from a two year growth study.

1) there are interspecific differences in annual and seasonal above ground biomass production.

2) there are differences in above ground biomass production and reproductive success within and between species over an altitudinal gradient.

3) there are significant differences in the annual and seasonal soil moisture conditions between sites dominated by different species.

4) there are significant differences in the soil nutrients levels between sites dominated by different species.

The results of the growth study (chapter 2) indicate that there is significant seasonal and annual differences in biomass production between species and that differences also occur within and between species over an altitudinal gradient. However both the productivity and the productivity ranking of the species was found to change from season to season and from year to year. Analysis of the peat core through a bolster dam (chapter 5) showed unequivocally the occupancy of this site by bolsters for at least 800 years. This site today shows an intricate mosaic of three bolster species with no evidence of differential height growth by any species. From these data it appears that there is little chance of species elimination due to differential growth rates between species without major climatic change.

Cushions invading bare areas were found to grow at relatively uniform rates (6.7-20.0 mm/year) and recruitment was continuous (assuming that size reflects age).

Soil moisture conditions were found to be above field capacity at all sites for most of the two year period, although the P. colensoi and D. minimum subsites on Mt. Field West did fall below field capacity for a short periods. On Mt. Wellington soils were at saturation for longer periods than the other sites and this may account for the slow growth rates recorded for A. forsteroides compared with the sites at Mt. Field.

All sites showed uniformly low soil nutrient levels, low pH and high organic matter. The processes of mineral mobilization within soils are largely a result of soil microbial activity. This activity is retarded by low temperature, low pH and poor aeration (Sparling 1985). Furthermore, if the percentage of organic carbon greatly exceeds total nitrogen then the activity of the microbial population is severely curtailed or stopped (Vaughan and Ord 1985). The percentage organic carbon was not measured in the soil analysis but the percentage organic matter (table 2-4) suggest that the C:N ratio in the cushion

peats would be very high. In addition to the low decomposition rates, available phosphorus is very low under conditions of low pH (Swift et al. 1979). Haag (1974) considered that low nutrient regimes may partially explain the high proportion of perennial plants in tundra systems, since those species can accumulate a nutrient pool over time from deficient environments.

From these data it seems that neither soil moisture (i.e. drainage) conditions nor a soil fertility gradient adequately explains the distribution patterns of the four bolster species growing on peat substrates at Mt. Field. What is evident from the data is the broad environmental overlap of the habitat of the bolsters. While P.colensoi and D. minimum can occupy very well drained sites, the sites monitored in the growth experiments were only slightly better drained than the other subsites on Mt. Field West. Soil nutrient levels were also very similar between species.

The data support the observation that bolsters occupy boggy sites and that P. colensoi and D. minimum can occupy better drained sites relative to the other bolster species (Kirkpatrick 1983, Kirkpatrick et al. 1985). However as to whether the overall distribution patterns of the cushion species are controlled by soil fertility, the data is equivocal. Within the relatively small geographic area of Mt. Field no species differentiation was evident (cf. Kirkpatrick 1982, Kirkpatrick et al. 1985).

Likewise interspecific competition between bolster species appears to play little role in determining species occurrence. An alternative hypothesis is that the present distribution of the bolster species reflect the high temperature limit to successful persistence (i.e. the altitude at which the bolsters are overtopped and displaced by taller species) and the past climatic history.

The BIOCLIM analysis indicated that while there was a large overlap in the annual temperatures of the sites occupied by the four bolster species there was a decrease in mean temperature of the sites occupied by the species (D. novae-zelandiae > A. forsteroides > D. minimum > P. colensoi, figure 4-1). This accords with the observed altitudinal relationships between species where in any particular area D. novae-zelandiae occurs at the lowest altitudes and P. colensoi at the highest. At the lower altitude limits of D. novae-zelandiae and A. forsteroides periodic fires appear to be necessary to reduce the taller vegetation to allow the persistence of these species. There is a significant rise in the

climatic tree line across the state from 750 m on the west coast to 1400 m in the central north east of the state (Kirkpatrick 1982). There is a consequent rise in the altitude of the subalpine and alpine zone across the state in which cushion vegetation occurs.

The absence of D. novae-zelandiae and D.minimum from the eastern Central Plateau and the north east highlands (figure 1-1) may be a result of restriction of these species ranges during the last ice age. If only A. forsteroides survived in the Last Glacial in the north east then the present distribution pattern may reflect a transitory stage toward the full occupation of potential habitat in the future. Within the limits of the BIOCLIM model the predictions supports this hypothesis (figure 4-4). The predicted distribution of the species ranges are poor fit to their actual ranges but the correspondence is better at the 'marginal' level (e.g. the model correctly predicts A. forsteroides habitat in central Tasmania, compare figures 1-1 and 4-4). At full habitat occupancy D. novae-zelandiae and A. forsteroides would have very similar distribution patterns as could be expected from similar temperature optimum (figures 4-1 and 4-4). D.minimum would be slightly more wide spread than at present while the distribution of P. colensoi would be little changed. It may be that the apparent replacement series seen in the bolster species is merely transitory.

10.2 Community dynamics

The second part of this thesis examined the dynamics of mosaic bolster heath communities. Initially two hypothesis were proposed.

1) that the changes in the vegetation from bare ground to mosaic bolster heath followed the classic facilitation model.

2) that the mosaic bolster heaths were stable in the mid to long term (5-1000 years).

Analysis of the revegetation of a series of drained tarns showed that the facilitation model did not hold in these communities. There was an almost complete lack of pioneering species and species tended to accumulate rather than undergo seral replacement. Such situations are better described by the inhibition/ tolerance models of Connell and Slatyer (1977).

A series of five year old photopoints in the establishment, mature and degenerate phases of the mosaic bolster community support this conclusion. In the establishment and degeneration phases of the bolster communities environmental factors rather than competition play the predominant role in determining community composition. This predominance of environmental factors over biotic has been described previously in low productivity environments (Bliss 1962, Webber et al. 1980). Competition has been suggested as important in determining community composition of alpine communities (del Moral 1983). Data from the photopoints clearly shows that large cushions (>5 cm^2) out compete smaller cushions. However the growth studies (chapter 2) and the observation that even within complex mosaics one cushion species never overgrows another indicates that competition effects between large individuals are either weak or regularly fluctuate.

Analysis of seedling recruitment into mosaic bolster heath showed no substrate preference except in one plot where P. lawrencii seedlings had less than expected survival on A. forsteroides. All other species exhibited no substrate preference. It is not possible to say from these data if establishment is a random event or not but Weir and Wilson (1987) have recently shown that microenvironmental factors determine small scale pattern in community distribution in cushion communities growing on mineral soils in New Zealand.

Data from the analysis of the peat core showed that mosaic cushion heath can persist in an area for long periods (at least 800 years). Within such areas changes in the water table can lead to small scale changes (<50 m^2) in species dominance. The general tendencies for mosaic bolster heath, seen from this core and the profiles mapped by Kirkpatrick and Gibson (1984), is to raise the water table and gradually subsume other vegetation types and the surrounding block streams.

A recent successional study from alpine New Zealand showed a cushion mire expanding into a grassland (Lough et al. 1987),. While this appears to be rare in New Zealand (Dobson 1979) it commonly occurs in Tasmania. The rate of expansion of D. novae-zelandiae in the Maungatua mire (2.9 mm/year diameter increase) is much slower than that recorded for A. forsteroides and P. lawrencii in open situations on peat soils (6.7-20.0 mm/year, chapter 3) but is within the range found for D. minimum seedlings colonizing rock and mineral soils (0-7 mm/year).

An 11 year study in the high alpine cushion field of the Old Man Range (Roxburgh et al. 1988) found an absence of pioneering species and supported the tolerance/ inhibition models of succession (Drury and Nisbet 1973, Connell and Slatyer 1977). These results accord with both the studies on the revegetation of drained tarns and the permanent photopoints (chapter 7).

Attempts to investigate community dynamics by the analysis of spatial pattern proved unsuccessful due to the limitations of the analytical techniques. As yet there appears to be no suitable technique to analyse data collected from a series of contiguous quadrats (e.g. cover, basal area, frequency, presence). Two-dimensional spectral analysis fails to split pattern into its two components, clump size and interclump distance. It appears that this discrimination is possible with the use of mapped point data (Diggle (1979) and Ripley (1977)).

10.3 The functional significance of the cushion form.

The third section of this thesis investigated the functional significance of the bolster form. World wide there is remarkable convergent evolution of unusual life forms in stressful habitats. Examples include the chaparral shrubs of the dry Mediterranean climates (Mooney and Dunn 1970), the giant rosette plants of the tropical zone (Smith and Young 1987) as well as the cushion plants of the alpine zone of the southern hemisphere (Gibson and Hope 1986). All of these studies have suggested that the particular life form represents a syndrome of interrelated physiological and morphological characters that buffer the plant against extreme environments. The chaparral shrubs have evolved in response to very hot temperatures and limited access to water (Mooney and Dunn 1970), the giant rosette plants grow in habitats characterized by extreme diurnal environmental fluctuations (Smith and Young 1987) and cushion plants reach their maximum development in cold windy environments (Wardle 1985).

Two aspects of the cushion form were investigated, (a) the structural anatomy of the four Tasmanian bolster species and the degree to which this has undergone convergent evolution, and (b) the thermal properties of cushions in relation to root and seedling freezing.

The ability of ground layer plants to exceed air temperature by 10° C or more is well known (Molgaard 1982, Spomer 1964, Fischer and Kuhn 1984) and as a

result plants in this layer are able to extend many hundreds of metres above the tree line (Wardle 1974). The ability of Tasmanian cushion plants to achieve surface temperatures well in excess of ambient was demonstrated for A. forsteroides in chapter 8. To fully understand this phenomenon would require the undertaking of detailed studies of photosynthesis and the water use patterns of these species. In the absence of such data it was suggested that the thermal warming of the cushion surface under conditions of low ambient temperature would be a significant advantage in allowing photosynthesis to occur under clear conditions of low ambient temperature. Plants growing under such conditions must also deal with such problems as overheating (Wardle 1974). In other environments it has been found that adequate soil water supplies and an efficient water transport system allow plants to actively grow under conditions of very high temperature (Fisher 1952).

The anatomy of the four bolster species showed features consistent with efficient transport systems (a multitude of veins or lack of a palisade layer and sunken stomata). Data from the growth studies (chapter 2) showed soil moisture conditions were generally well above field capacity. If the freezing of the soil occurs in winter when the cushions are exposed water stress may develop. Freezing of the peats on Mt. Field West has been demonstrated but the frequency and duration of such events needs further quantification. Tranquillini (1982) suggests that soil moisture becomes unavailable to plants when soil temperature drops below 0° to -1°C. While such conditions undoubtedly occur no damage to bolsters attributable to winter desiccation have ever been recorded (W.D. Jackson, J.B. Kirkpatrick pers. comm.).

Anatomical features which could be correlated with the avoidance of winter desiccation (such as sunken stomata fill with wax, or a thick trichome layer) are entirely lacking in the bolster species examined. These observations suggest that if winter water stress does occur then bolsters respond by simple stomatal closure and the length of time that such conditions prevail is insufficient to result in tissue damage. Further more the surface layers of bolsters warm very rapidly and these layers can also hold considerable amounts of moisture. Hence if soil freezing did occur the thawing of the top layers of bolster (which include numerous adventitious roots in most species) would occur relatively rapidly. Winter desiccation is therefore unlikely to be a significant environmental limit to the occurrence of bolster species in the Tasmanian environment. Similar

results have been reported for tree species from mainland Australia (Slatyer 1976, Tranquillini 1982).

The internal anatomy of the four bolster species failed to show the high degree of convergence seen in their morphological characters. Similar results have been reported from a study of a number of cushion plants from the dry puna region of South America (Ancibor 1980).

The second feature of the cushion form studied was their thermal properties in relation to root freezing. Root freezing occurs in all species at temperatures between 0° and -5° C, thus all are classified as stress avoiders (Levitt 1972). Thermal profiles from the freezing chamber experiments suggest that the thermal capacity of the bolsters is such that root freezing would be an extremely rare event in alpine Tasmania. Similarly given the thermal capacity of the peat soil, root freezing would also be extremely rare in seedlings (even though their root systems are quite close to the soil surface). Some variation was found in the freezing temperature of A.forsteroides (-1.0° C to -4.6° C) using a standard method. This implies that root freezing temperatures may undergo some hardening or that it might be dependent on root turgor (if roots are somewhat dehydrated then a higher solute potential would result in a lower freezing temperature).

10.4 Conclusions

The inherent slow growth rate of bolster species restrict their distribution to low productivity environments where taller species are excluded or grow only slowly. D. novae-zelandiae and A. forsteroides, which descend to the lowest altitudes, appear to require fire to reduce competition from graminoids and shrubs at their lower distributional limits (Kirkpatrick 1983, personal observation).

The four species studied show overlapping distributional patterns indicating broad environmental tolerances. The results of the growth study support this contention. Differences in biomass production could not generally be related to soil moisture, soil nutrients, altitude or temperature within or between species (however not all species occurred at all sites). The exception to this may be the depressed growth rate of A. forsteroides on Mt. Wellington (cf. Mt. Field) in response to anaerobic soil conditions. All species are capable of growth in

nutrient poor, acid environments. It is suggested that the major determinant of cushion distribution in Tasmania is past climatic history and species temperature tolerances determining the bolsters limits (probably through competitive interaction with taller growing species).

The role of competition in determining floristic composition in bolster communities appears to be variable. The magnitude of its influence appears correlated with the productivity as has been suggested previously (Huston 1979, del Moral 1983). In the most stressed environments studied (the invasion of rocky substrates by D. minimum) competition appeared very much less important than abiotic factors. In closed communities at the more equitable sites (in terms of soil moisture etc) competition appeared to act strongly at the recruitment phase but plays a less significant role once establishment had occurred. The still more productive lower limits of cushion distributions are likely to be controlled by competition from shrubs and graminoids.

The ability of bolsters to absorb significant amounts of heat has implications for extended photosynthesis. The thermal absorption of the bolster species could allow extended periods of photosynthesis to occur under suboptimal ambient conditions (Longton 1970, Seppelt and Ashton 1978). The leaf turnover rate of Tasmanian bolster species (0.5-2.5 years) is faster than those reported from the northern hemisphere (2-4 years). This may be a result of the much longer growing season in Tasmania compared with the alpine and tundra regions of the northern hemisphere. The insulation provided by the bolsters and that of the peat soil suggests that root layers would only rarely, if ever, reach the freezing temperature (-1° to -5° C) under present climatic conditions.

Wardle (1986) has suggested that the cushion lifeform is particularly well adapted to cool windy environments without extremes of cold. The data reported in this thesis support this view showing inherently slow growth rates, tolerances to ~~high~~ low pH and low nutrient environments, evidence for opportunistic growth (likely to be due in part to the thermal properties of the cushions), and root freezing temperatures and thermal diffusivity of peats concomitant with survival under maritime rather than continental climates.

As with the tropical-alpine giant rosette plants, and the chaparral shrubs, the cushion life form appears to have evolved independently in widely separated areas at a variety of times (Mooney and Dunn 1970, Young and Adams 1987,

Gibson and Hope 1986). However the cushion genera Donatia and Phyllachne appear to represent very old Gondwanic elements, given the present distribution patterns of these groups in Tasmania, New Zealand and South America (Raven 1973, Wardle 1978). If this is the case then low productivity environments appear to have existed in all these areas for very long periods (Hill and Gibson 1986b, cf. Smith 1986).

As a basic tenet all research raises yet more questions, this thesis is no exception. Given the work reported in this thesis the most useful directions for that research are:

(a) the determination of the water use patterns of bolster species in relation to high surface temperatures, high soil moistures, the lack of a xeromorphic anatomy, and the possibility of winter drought.

(b) the determination of photosynthetic light and temperature responses in relation to the thermal characteristics of the cushions.

(c) the determination of the temperature optimums and the full extent of the bolster species range by transplant experiments across wide altitudinal and geographic gradients.

(d) the determination of the extent to which the scleromorphic anatomy of the bolster species is related to nutrition.

(e) the determination of the genotypic differentiation of the Tasmanian, New Zealand and South American species of Donatia and Phyllachne.

(f) the determination of the effect of root oxygen levels on biomass production between the bolster species.

The resolution of these questions would test the interpretations of the cushion species biology made in this thesis in relation to distribution patterns, vegetation processes, and functional significance of the bolster form.

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APPENDIX 1

List of papers published resulting from PhD and other research. (Copies bound in back, unless otherwise indicated)

Gibson, N. (1984) Effects of trampling on alpine bolster communities at Mt. Field National Park, Tasmania. Papers and Proceedings of the Royal Society of Tasmania 118: 47-52.

Gibson, N. (1986) Conservation and management of Huon pine in Tasmania. Wildlife Division Technical Report 86/3 NPWS, Tasmania 91pgs. (copy not included)

Gibson, N. (1988) A description of the Huon pine forests of the Prince of Wales and King Billy Ranges, Tasmania. Papers and Proceedings of the Royal Society of Tasmania 122 : in press. (copy not included)

Gibson, N. and Hope, G.S. (1986) On the origins and evolution of Australasian cushion plants. IN Flora and fauna of alpine Australasia B.A. Barlow (ed) CSIRO, Melbourne pp 63-82.

Gibson, N., Kiernan, K.W. and Macphail,M.K. (1987) A fossil bolster from the King River, Tasmania. Papers and Proceedings of the Royal Society of Tasmania 121: 35-42.

Gibson, N. and Kirkpatrick, J.B. (1985a) A comparative study of the cushion plant communities of New Zealand and Tasmania. New Zealand Journal of Botany 23: 549-566.

Gibson, N. and Kirkpatrick, J.B. (1985b) Vegetation and flora associated with a localized snow accumulation at Mt. Field, Tasmania. Australian Journal of Ecology 10:91-99.

Gibson, N., Williams, K., Marsden-Smedley, J., Brown, M.J. (1987) Regeneration characteristics of a swamp forest in northwestern Tasmania. Papers and Proceedings of the Royal Society of Tasmania 121: 93-100.

Brown, M.J., Bayly-Stark, H.J., Duncan, F., Gibson, N. (1986) Tetratheca gunnii Hook f. rediscovered on serpentine soils near Beaconsfield, Tasmania. Papers and Proceedings of the Royal Society of Tasmania 120: 33-38.

Hill, R.S. and Gibson, N. (1986a) Input of potential macrofossils into Lake Dobson, Tasmania. Journal of Ecology 74: 373-384.

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APPENDIX 2

Determination of soil moisture curves.

A2.1 Introduction

It was initially believed that soil moisture conditions might be drastically different at the different sites where the growth experiment was established (Chapter 2). Three bulked soil samples were collected from each site each month from each of three depths 0-5 cm, 5-10 cm, 10-20 cm. These were air dried and percentage soil moisture was calculated on a dry weight basis. It was originally intended to determine the soil moisture characteristics for each of these soils using pressure membrane apparatus. It became evident, however, that soil moisture was rarely limiting in any of the sites selected for the growth study. Indeed the lowest percentage soil moisture recorded was 91% with most in the range of 150-600%. It was therefore considered that detailed work on determination of soil moisture curves was not warranted.

A2.2 Methods and Results

As an alternative to the pressure membrane technique the filter paper method of Hamblin (1981) was used. This involved the use of standard Whatman No.42 filter papers which have been shown to be remarkably accurate in absorption properties in a variety of soils (Fawcett and Collis-George 1967, Hamblin 1981). Briefly the method involved placing a filter paper in a series of sealed containers with soil of known (and varying) water content. After equilibrium had been reached the filter papers were weighed then dried, then reweighed and percentage moisture determined. A curve can be constructed for each soil showing percentage soil moisture and filter paper water content. This was done for soils from each of the growth study sites with between 10-40 points being determined for each soil.

Hamblin (1981) has produced a regression for filter paper water content versus water potential which was highly reproducible over a series of batches of filter papers. The regression he reported is however incorrect. The regression was recalculated using the data of Fawcett and Collis-George (1967) and took the form

$$Ln(Ym) = -4.558 + -3.4377.ln(F)$$
$$(r = -0.9936 \quad P<0.001)$$

where F is the gravimetric water content of the filter paper (fraction of dry weight) and Ym is the matrix potential of the soil (MPa).

From these data and the assumptions that field capacity was equivalent to 0.03 MPa and wilting point was equivalent to 1.5 MFa, soil matrix potential could be calculated from the monthly soil moisture data. It was found that soil moisture only fell below field capacity on one occasion at one site and it was generally above saturation (Chapter 2).

APPENDIX 3

Comparison of cushion growth rates between Tasmania and Macquarie Island

A3.1 Introduction

Huntley (1972) reported high growth rates (shoot production 850-960 g/m^2) for the cushion species Azorella selago from subantarctic Marion Island. Given the much lower growth rates reported from Tasmania (Chapter 2) and New Zealand (Bliss and Mark 1974) and the cold maritime climates of these islands (Huntley 1972, Jenkin 1975) these results appear anomalous. During the 1984/85 summer it was decided to test this hypothesis by undertaking growth studies on the cushion species Azorella selago and Colobanthus muscoides on Macquarie Island. These studies were essentially similar to those reported in chapter 2 and for comparative purposes measurement of shoot production by A. forsteroides on Mt. Wellington was continued over the 1984/85 summer.

A3.2 Study areas

This study was carried out at the Mt. Wellington site previously described and three sites on Macquarie Island. Colobanthus muscoides was studied at a lowland site and Azorella selago at two upland sites (table A3-1).

Macquarie Island (54° 30' S, 158° 57' E) is an isolated subantarctic island composed largely of Tertiary basalts and related rock types apparently formed by sea floor uplift (Griffin and Varne 1980). The island is 34 km long and up to 5 km wide. From narrow beaches or raised beach terraces it rises steeply to an undulating or hilly upland plateau from 200 - 300 m in altitude with higher peaks to 433 m. The climate is uniformly cold, wet and windy. Mean annual precipitation is 1010 mm over 330 days; mean wind speed 10.3 m/sec; mean annual temperature 4.5° C with a mean range of 3.3° C and mean diurnal variation of about 1.6° C (Jenkin and Ashton 1970).

Forty-five species are represented in the vascular flora (Seppelt et al. 1984). There are no trees or shrubs with the tallest plant being the maritime tall tussock grass Poa foliosa.

Table A3-1 Details of species and site descriptions for Tasmania and Macquarie Island.

Site	Species	Altitude	Slope	Aspect	Drainage
Tasmania:					
Mt. Wellington	Abrotanella forsteroides	1150	0°	nil	poor
Macquarie Island:					
Isthmus	Colobanthus muscoides	6	5°	270	very good
Perseverance Bluff	Azorella selago	235	5°	90	moderate
Mt. Elder	Azorella selago	330	2°	110	moderate

The cushion forming Colobanthus muscoides is a species characteristic of the maritime communities growing on coastal rocks (Taylor 1955). A study site was selected on a rock stack on the west side of the isthmus near the ANARE base at the northern end of the island, and is here referred to as the Isthmus site.

The other major cushion forming species, Azorella selago is abundant in the more exposed upland areas of the island (Taylor 1955, Ashton and Gill 1965). Two study sites were established. The first near Perseverance Bluff (235 m) is a protected Azorella selago fjaeldmark/Pleurophyllum hookeri herbfield ecotone. The second was established in a more exposed Azorella selago fjaeldmark on the northern flanks of Mt. Elder (330 m).

A3.3 Methods

A3.3.1 The Environment

The study was run over 135 days on Macquarie Island (24 October 1984 - 7 March 1985) and over 159 days on Mt. Wellington (1 November 1984 - 8 April 1985). Rainfall was collected on a monthly basis at the two plateau sites on Macquarie Island (27 cm diameter rain gauges). The Isthmus site was located approximately 30 m from the Macquarie Island Meteorological Station from which rainfall and temperature data were obtained. Temperature and rainfall data were measured on Mt. Wellington as previously outlined (chapter 2). At all sites monthly soil temperature profiles, soil moisture determinations and temperature integrator data were obtained as described in chapter 2.

A3.3.2 Net Primary Production

Net primary production was measured in two ways. On Mt. Wellington growth was measured as described previously (chapter 2). On Macquarie Island modified Clymo (1970) growth pins were used to determine shoot extension during the study period. Either 30 or 50 pins per site were inserted to a depth of approximately 15 cm. The exposed 5 cm of pin was remeasured at the end of the study using a caliper and the difference was taken to indicate shoot height increase. Shoot density, leaf density and leaf weight were treated as for A. forsteroides. Modified clymo pins were also set up on Mt. Wellington, however these were interfered with before growth measurements were taken, so no direct comparison of the two methods was possible.

It was necessary to use clymo pins on Macquarie Island since the environmental and growth measurements were made by Dr Rod Seppelt (Antarctic Division) after the departure of the resupply voyage. This method allowed quick measurement of growth to be made which was of considerable advantage given the large program being undertaken by Dr Seppelt.

A3.4 Results and Discussion

A3.4.1 The Environment

There is now no permanent meteorological station on Mt. Wellington. Table A3-2(a) shows long term means and the 1984/85 maximum and minimum temperature and rainfall data. Table A3-2(b) shows the 1984/85 data from the Macquarie Island Meteorological Station as well as the rainfall measurements from the two plateau sites.

The environment on Mt. Wellington is warmer but less equable than Macquarie Island. The extreme ranges of temperature were of the order of 30° C on Mt. Wellington but only 13° C on Macquarie Island. On Mt. Wellington the monthly extreme temperatures were both higher and lower than those experienced at all sites on Macquarie Island for all months with the possible exception of November (allowing 2° C/300 m lapse rate). The extreme maximum temperature of 14.4° C in December is an all time record for Macquarie Island. Wind speed is the other major difference between the two areas. No long term wind speed data are available for Mt. Wellington; from short term studies it is estimated to be of the order of 3-5 m/sec (L. Gilfedder pers. comm.). Wind speeds on Macquarie Island are 2 to 3 times this. On Macquarie Island wind speed increases with increasing altitude, averaging 32% higher on the plateau (Jenkin 1975). During the study wind runs were significantly below the long term average on the island.

Rainfall was well above the ten year mean during 1984/85 on Mt. Wellington. Rainfall data from Macquarie Island indicates a generally higher rainfall on the plateau and a moderate degree of variability between sites.

Soil moisture was above field capacity and generally at saturation on Mt. Wellington and the two Macquarie Island plateau sites throughout the study.

Table A3-2(a) Climatic data from Mt. Wellington. Ten year means (1961-1972) and 1984/85 maximum and minimum temperature and rainfall data shown in parentheses. (Bureau of Meteorology pers. comm.).

	OCT	NOV	DEC	JAN	FEB	MAR.
Mean temperature (°C)	3.7	4.7	6.6	8.6	9.3	7.7
Mean maximum	7.1	8.4	10.5	2.8	13.3	11.3
Mean minimum	0.2	1.0	2.6	4.4	5.2	4.1
Extreme maximum	(21.4)	(26.1)	(26.1)	(26.6)	(23.3)	(28.0)
Extreme minimum	(-3.9)	(-2.9)	(-1.1)	(-0.3)	(-2.9)	(-3.9)
Rainfall (mm)	61	71	76	61	71	64
Rainfall 1984/85 (mm)	(113)	(118)	(100)	(143)	(124)	(67)

Table A3-2(b) Climatic data from Macquarie Island 1984/85 (Bureau of Meteorology, pers. comm.). Rainfall figures from plateau sites in parentheses - Perseverance Bluff, Mt. Elder.

	OCT.	NOV.	DEC.	JAN.	FEB.
Mean temperature (°C)	4.3	4.9	7.1	8.3	8.1
Mean maximum	6.1	6.6	9.1	9.9	9.1
Mean minimum	2.4	3.1	5.1	6.8	6.5
Extreme maximum	7.5	8.7	14.4	12.0	11.1
Extreme minimum	-0.6	-2.8	1.9	4.5	4.0
Rainfall (mm)	104	56	100	83	75
Rainfall plateau sites (mm)	-	(90/85)	(105/117)	(81/92)	-
Mean wind speed (m/sec)	7.7	7.2	5.0	5.5	6.9

Soil at the Mt. Wellington site absorbed a much higher thermal load more rapidly and held it for a longer period than any of the Macquarie Island sites (figure A3-1). The lowland Isthmus site on Macquarie Island is quite different from the two plateau sites in both the amount of energy absorbed and the onset of cooling. The two plateau sites were very similar to each other and appear to have passed their peak thermal loads by the end of February. The more variable climate at the Mt. Wellington site is highlighted by a temporary drop in soil temperature during the latter part of February (and as was seen in January 1983, see Chapter 2).

Data from the temperature integrators located just below the cushion surface showed similar trends (figure A3-2). The Mt. Wellington site had a much greater thermal input, which was variable from month to month, but which increased throughout the study period. The Isthmus site showed gradual temperature increase throughout the study, while the two upland Macquarie Island sites showed considerably less thermal input and had apparently peaked by the end of January. Soil temperature at the three Macquarie Island sites was less variable than Mt. Wellington. Temperature data from all sites recorded by the two deeper sensors showed a similar pattern to the surface probe, but were dampened due to the insulating properties of the soil and cushion peat (see figure 3-7).

The temperature integrator data from Macquarie Island showed cushion surface temperature greater than 15° C for up to 18% of the time (figure A3-2) while ambient temperature never rose above 14° C. On Mt. Wellington cushion surface temperature was above 20° C for up to 15% of time, considerably in excess of that expected from ambient temperatures. The apparent heat sink properties of the cushions were investigated further and the results are reported in Chapter 8

A3.4.2 Net dry matter production

Net dry matter production was greatest for Colobanthus muscoides at the Isthmus site, followed by Abrotanella forsteroides from Mt. Wellington, then Azorella selago on the two plateau sites (table A3-3). This pattern shows that dry matter production is not completely explained by the decrease in total energy (figure A3-2).

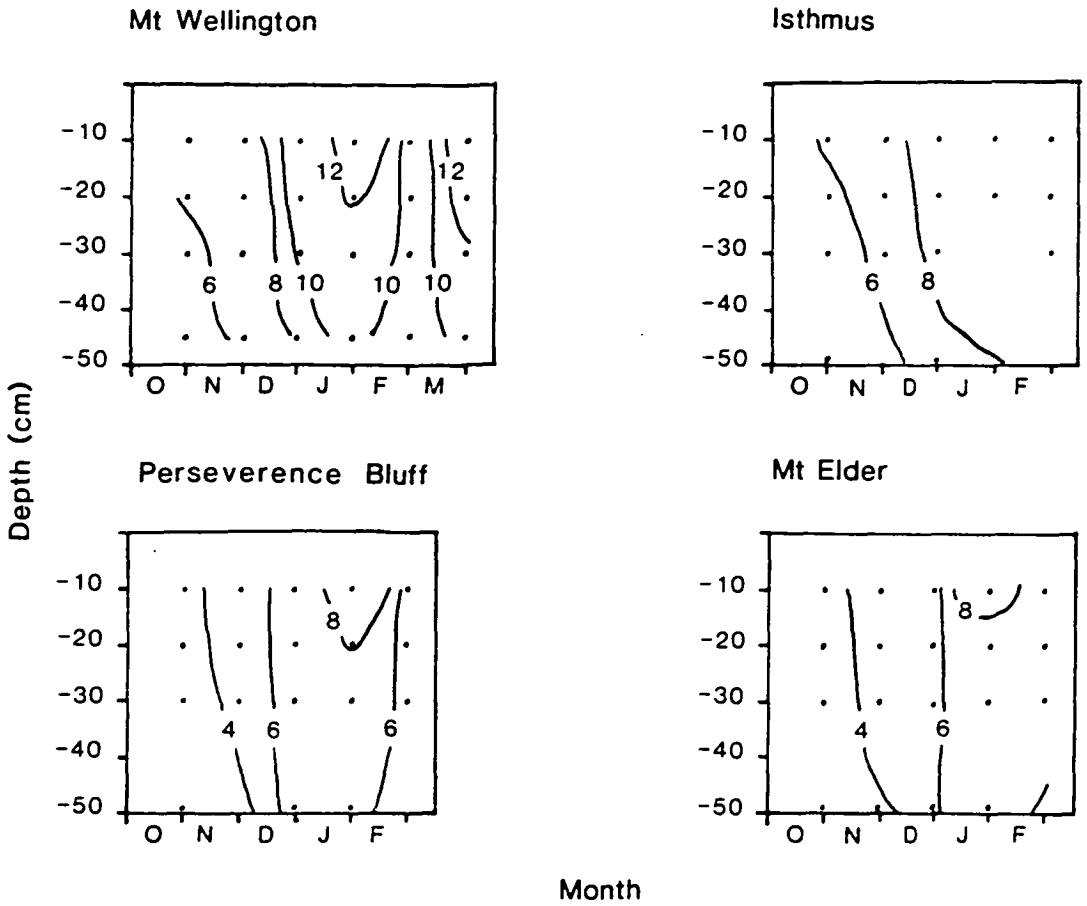

Figure A3-1. Soil temperature profiles for three sites on Macquarie Island (Isthmus, Perseverance Bluff, Mt. Elder) and the Mt. Wellington site recorded over the 1984/85 summer. Dots indicate depth (cm) and time of sampling.

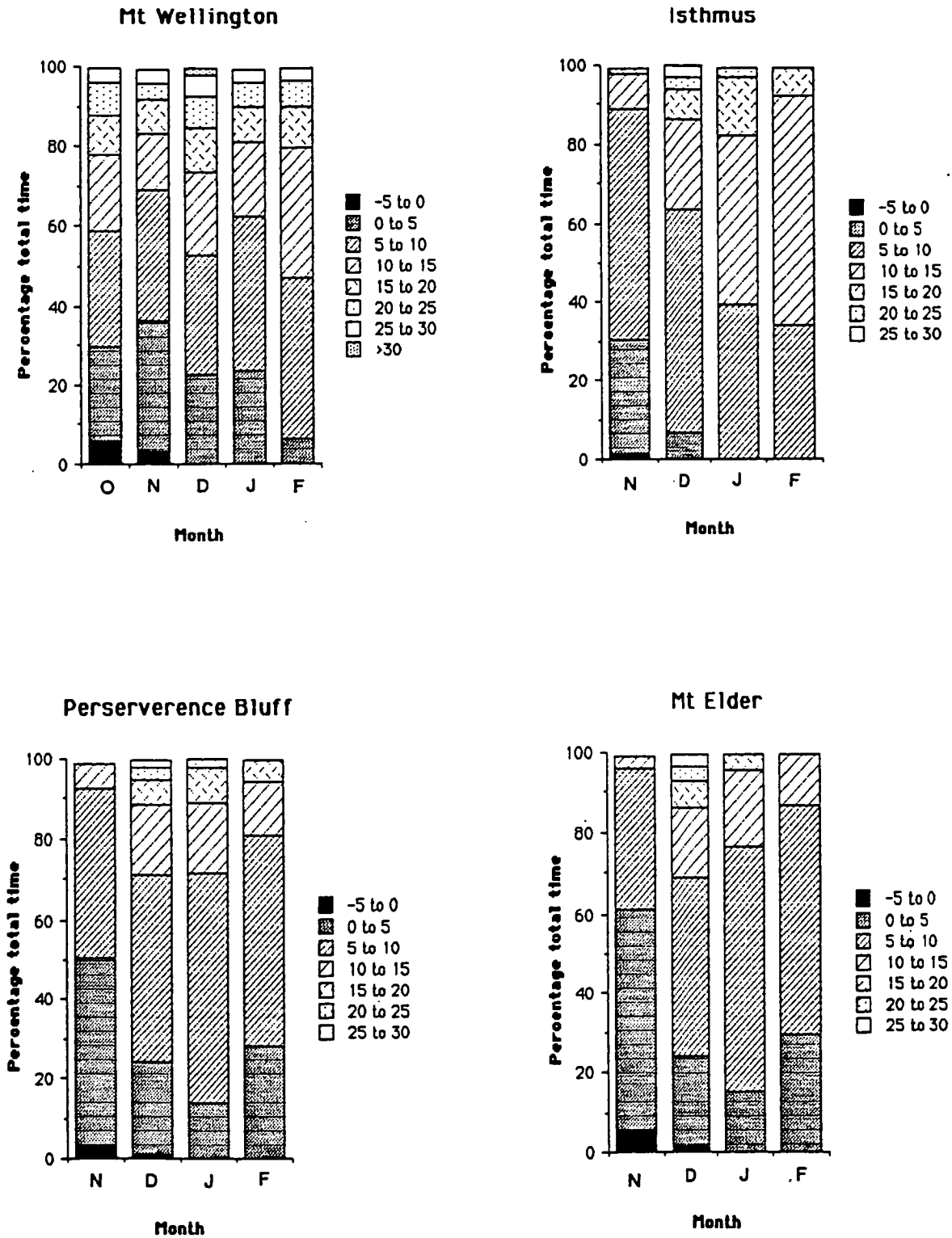

Figure A3-2. Temperature integrator data from sensors located just below cushion plant surfaces for three sites on Macquarie Island (Isthmus, Perseverance Bluff, Mt. Elder) and the Mt. Wellington site recorded over the 1984/85 summer. Percentage of total time spent in each of eight 5° C temperature intervals shown by month.

Table A3-3 Net primary production data for cushion plants on Macquarie Island and Tasmania. Data refer to a 135 day period on Macquarie and to 159 days in Tasmania.

SITE	MACQUARIE ISLAND			TASMANIA
	Isthmus	Perseverance Bluff	Mt. Elder	Mt. Wellington
Species	C. muscoides	A. selago	A. selago	A. forsteroides
Shoot density (/m^2)	108 273	93 170	91 727	105 360
Increase shoot length (mm)	2.7	1.5	2.7	1.0
No. of new leaves	9.6	1.9	1.9	16.7
Total shoot production (g/m^2)	268	124	162	281
Mean shoot production (g/m^2/day)	2.0	0.9	1.2	1.8

All three species are characterized by very high shoot densities and small but variable amounts of shoot extension. This ranged from 1.0 mm for A. forsteroides to 1.5-2.7 mm for A. selago to be 2.7 mm for C. muscoides (Table A3-3). The data from Macquarie Island measured by Clymo pins should, however, be treated as tentative. It was found that 25% of pins recorded negative growth (i.e. these pins became more exposed rather than being subsumed into the cushions, mean = 2.2 mm). Given the large range of measurements (0.3 - 29.9 mm), this probably resulted from interference by skuas, inquisitive savaging gulls common in this area. The alternate possibility is frost heaving but it is difficult to account for such a range of negative measurements by this method. The pins that recorded negative growth were excluded from the analysis. Detailed studies such as those carried out in Tasmania are needed to confirm estimates of A. selago and C. muscoides growth.

Bliss and Mark (1974) reported growth rates of c. 0.8 g/m^2/day for high alpine cushion vegetation in New Zealand. This figure is similar to that found for A. selago on the upland sites on Macquarie Island but considerably lower than for C. muscoides from the lowland site or for A. forsteroides from Mt. Wellington (table A3-3). The figures from both Macquarie Island and Mt. Wellington were taken over only a part of the growing season and therefore are likely to be somewhat higher than if measured over a full growing season since growth is likely to be slower both at the beginning and end of the season.

The data of Huntley (1972) for Azorella selago from Marion Island are very different (table A3-4). He reports net primary production figures of 3.8-4.0 g/m^2/day. These are three to four times those found in this study. Indeed the cushion growth rates recorded by Huntley (1972) are similar to those reported for Poa foliosa tussocks at 235 m on Macquarie Island (Hnatiuk 1978).

Shoot density reported from Marion Island is about one third that on Macquarie Island, implying that individual shoots are growing nine to twelve times faster on Marion Island. Nevertheless, height increase from fjaeldmark sites on Marion Island is similar (1.1 mm) to that reported here (1.5-2.7 mm, table A3-3), but new leaf production on Marion Island is reported to be 6-9 leaves compared to 1-2 found on Macquarie Island. A. selago in sheltered sites on Marion Island recorded an annual height increase of 6 mm/year which is similar to that reported from an unspecified site on Macquarie Island (6.4 mm) by Taylor (1955); these figures are three times that reported here from the A.

Table A3-4 Net primary production for Azorella selago from Marion Island. Data refers to a 255 day growing season at site 1 and a 225 day growing season at sites 2 and 3 (after Huntley 1972).

Site	1	2	3
Community	Herbfield	Fjaeldmark	Fjaeldmark
Shoot density (/m^2)	24 500	38 000	42 400
Total shoot production (g/m^2)	960	854	895
Mean shoot production (g/m^2/day)	3.8	3.8	4.0

selago fjaeldmarks. Given the depauperate nature of the vascular flora of subantarctic islands (Seppelt et al. 1984), it is reasonable to expect that species would occur over large sections of the environmental gradients. This may partially account for some of the differences reported for A. selago on Macquarie and Marion Island.

A3.5 General Discussion

Climatic data indicates that the alpine area of Mt. Wellington enjoys a warmer but less equable environment than that found on Macquarie Island. Soil temperature data suggest that the summer thermal input into the Mt. Wellington site starts earlier and though fluctuating is still increasing at the end of March. Thermal input is much greater than found on Macquarie Island (figures A3-1 and A3-2). The lowland site on Macquarie Island has a higher energy input than either of the plateau sites. The plateau sites are similar, and soil temperature appears to peak by the end of January. The plateau is often shrouded in mist, which would contribute to the lower energy input.

These differences are only partially reflected in the net primary production figures. A. forsteroides from Mt. Wellington showed similar productivity levels to C. muscoides from the lowland site on Macquarie Island on a daily basis. The lower than expected productivity of A. forsteroides can probably be accounted for by the more anaerobic conditions in which this species grows (chapter 2). Given the longer growing season experienced at Mt. Wellington A. forsteroides would be expected to produce more biomass than C. muscoides in a full year.

The upland A. selago sites produce about half the dry matter of C. muscoides and A. forsteroides. Between these sites however the higher productivity was achieved by the cooler more exposed sites(table A3-1 and A3-3, figure A3-2). Clearly although total available energy is important in determining the potential productivity of a site, environmental differences (such as soil moisture conditions) are also important. These differences may be quite subtle, as demonstrated by the difference in productivity between the A. selago sites which are superficially very similar except for the degree of exposure.

Huntley's (1972) data from Marion Island appears to be anomalous given that he sampled similar plant communities to those measured on Marion Island but recorded growth rates three to four times greater. These differences may be

related to site conditions, or differences in measurement technique or may be genotypically based given that shoot density on Marion Island was only 26-46% of that recorded for Macquarie Island. A comparative study of A. selago from a variety of subantarctic islands could elucidate the reason for the differences and may be useful in determining distribution routes and patterns in genetic variability of this species

Dynamics of a Tasmanian bolster heath string fen*

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Keywords: Alpine, Bolster plant, Cushion plant, Cyclic succession, Dynamics, Fen, String fen, Tasmania

Abstract

The string fen at Newdegate Pass, Mt. Field, Tasmania consists of dams composed of bolster heath and peat derived from bolster heath, and flark ponds with concave sides and usually rocky floors. The bolster heath has a smooth surface which consists of a complex mosaic dominated by *Donatia novae-zelandiae*, *Carpha rodwayi* and *Dracophyllum minimum*. The floors of the ponds usually support no macrophytes. The ponds situated on strong flow lines have shallower dams which are more often breached than those where flow is more diffuse. The ponds ultimately drain by tunnelling through the humified peat below the live roots of the bolster heath, and the exposed floors are colonized by bolster heath species. The underlying block stream has a topography partly independent from that of the string and flark features, which shift in both time and space.

Introduction

String bogs and fens, consisting of strings of relatively high relief and depressions or flarks often occupied by pools, are a widespread landform complex (Washburn, 1979; Sjörs, 1961; Moore & Bellamy, 1964). A large number of hypotheses have been formulated to explain their origin (Washburn, 1979). However, it seems likely that there is no single string bog/fen formation process, but rather that different processes with varying biotic, periglacial and gravitational components operate to produce similar landforms on different sites (Moore & Bellamy, 1974; Ives, 1941). The vegetation of the strings may be dominated by mosses, grasses, sedges, lichens, sclerophyll shrubs or trees (Sjörs, 1961; Boatman & Armstrong, 1968; Henoch, 1960; Moore & Bellamy, 1974; Burrows & Dobson, 1972; Ives, 1941; Walter, 1977). The flarks may be bare of higher plants or covered with a sparse growth of mosses, sedges or herbaceous hydrophytes. Many variants contain moss of the genus *Sphagnum* (e.g. Moore & Bellamy, 1974; Boatman, Goode & Hulme, 1981). In some cases the string and flark systems exhibit a high degree of resilience to disturbance (Ives, 1941), while in other areas there is evidence for erosional loss of string and flark pool complexes (Pearsall, 1956; Bower, 1960). Many authors have regarded these features as highly dynamic, especially when *Sphagnum* species are important in the vegetation.

This paper reports the results of our investigations into the characteristics and dynamics of an alpine string fen at Newdegate Pass, Mount Field, Tasmania (1 300 m above sea level at 42°40'S). At this location the strings are dominated by bolster plant species, the term bolster referring to chamaephytes which form hard cushions when growing individually and which fuse into gently undulating

* Species nomenclature follows Curtis (1963, 1967) and Curtis & Morris (1975) for gymnosperms and dicotyledons and Willis (1970) for monocotyledons except where authorities are given. Structural nomenclature follows Kirkpatrick (1983).

Vegetatio 58, 71–78 (1984).

mosaics when in interspecific or intraspecific mixture. Bolster plants have been referred to as cushion plants, a term that does not distinguish them from the softer cushion plants typical of the northern hemisphere alpine zone.

Our work was designed to test two alternative hypotheses. The first of these, advanced by Martin (1940) and supported in Jackson (1973, 1981), is that the bolster plant species are the major components in a cyclic successional process involving the damming of streams and soaks, and a later decay and invasion of bolsters by other shrub species as drainage patterns shift. The alternative working hypothesis is that the bolster species are simply occupying and slightly accentuating a fossil landscape created by congelliffuction processes during the Last Glacial.

Methods

The string bogs and vegetation at Newdegate Pass were mapped from panchromatic aerial photographs and field inspection. Cross-sections of the surface features and the underlying mineral surface were obtained in January 1983 using a dumpy level, Carr staff and a firm metal rod which penetrated easily through peat but not the non-organic substrate. The nature and depth of breaches that had occurred in the walls containing the flarks, the depth of organic material below pond outlets and the presence or absence of a lower possible escape route for water in the underlying rock surface about the outlets were recorded throughout the study area (Fig. 1).

A transect consisting of contiguous 35 cm ×

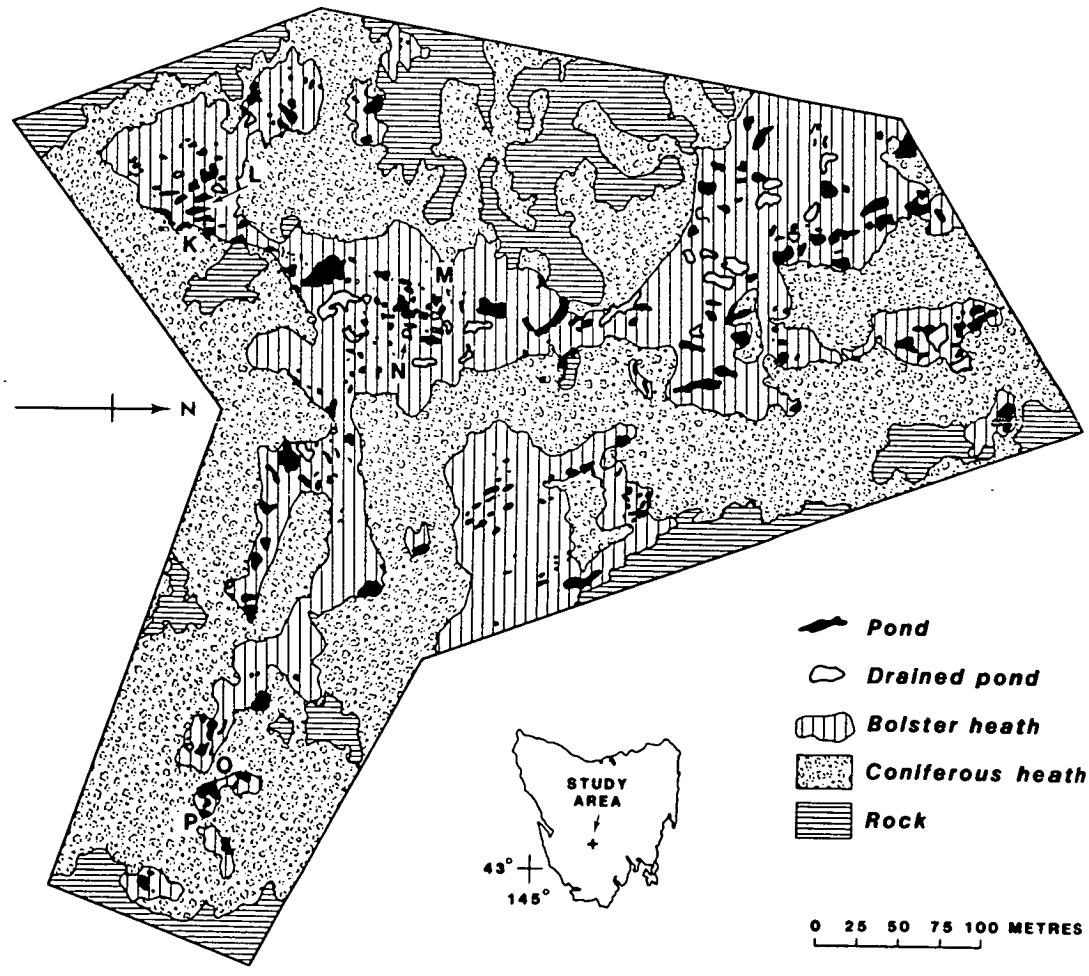

Fig. 1. Vegetation map of the study area showing breached and unbreached flark ponds and the location of transects.

35 cm quadrats was laid out through several typical strings and flarks. The covers of all vascular plant species within the quadrats were measured using 49 equal divisions in the quadrat as a guide.

Results and discussion

Vegetation

The string fens at Newdegate Pass are contained within a matrix of bolster heath which is largely surrounded by coniferous heath and lichen-covered dolerite boulders (Fig. 1, Plate 1). The string dam vegetation is shown in Figure 2. *Carpha rodwayi* W. M. Curtis is extremely important in these dams and is most abundant where the seepage is greatest, as are *Drosera arcturi* and *Oreobolus pumilio*. The bolster species *Dracophyllum minimum* and *Donatia novae-zelandiae* are major components of the dam vegetation whereas the morphologically similar *Abronatella forsteroides* is mostly absent from the dams. The softer *Pterygopappus lawrencii* is most prominent on the crest of the dams where the peat is least often waterlogged. A mat-forming lily, *Astelia alpina*, occasionally forms pure stands at the outlets of flark ponds. Where ponds have been drained to a depth greater than 15 cm below their previous high water level the dense prostrate mat of dam vegetation exhibits considerable necrosis, with *P. lawrencii* tending to become relatively more prominent despite suffering dieback. Where drainage reveals the floor of the pond, and the floor consists of organic material, *Carpha rodwayi* is the initial invader. Organic material on the floor of *ponds* is sparsely colonized by *Isoetes gunnii* where water is persistent or by *Myriophyllum penduculatum* and/or *Scirpus productus* where the pond occasionally dries. Most ponds have no higher plants on their floors, but have an algal scum covering both rocks and loose organic detritus.

Landforms

The shapes and sizes of the flark pools vary considerably (Fig. 1). Most are elongated along the surface contour line with the typical shape of the deeper pools being oblong-rectangular. Most pools are completely surrounded by peat walls up to 0.6 m high (Figs. 3–5). A mat of vegetation covers the outer part of the walls and extends to just below the outlet level on the inner part of the walls which are

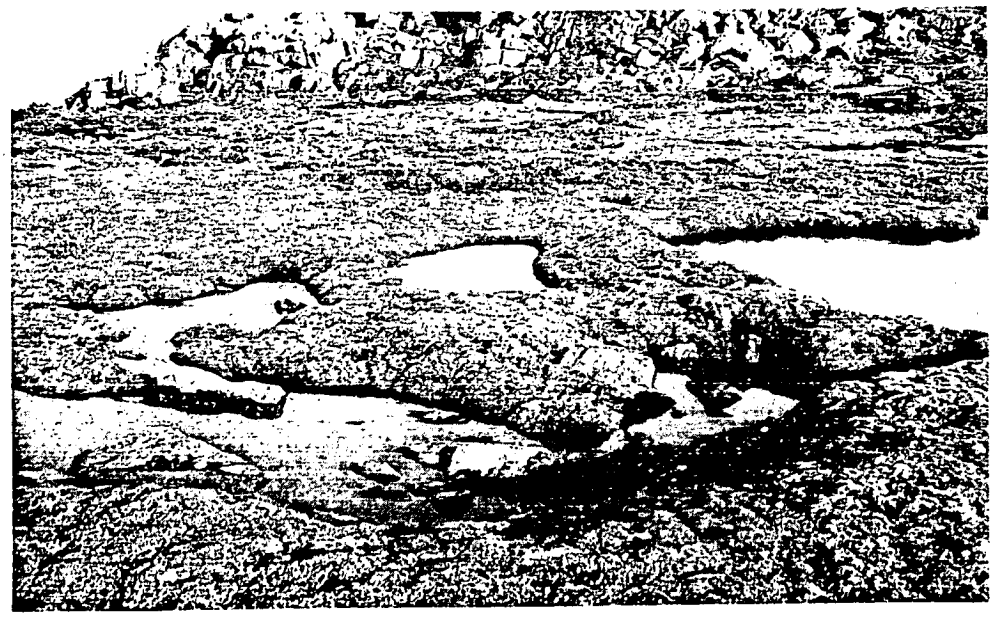

Plate 1. A small group of ponds. The difference in elevation between the two highest ponds is 0.5 m. A mat of bolster heath gives way to coniferous heath in the background.

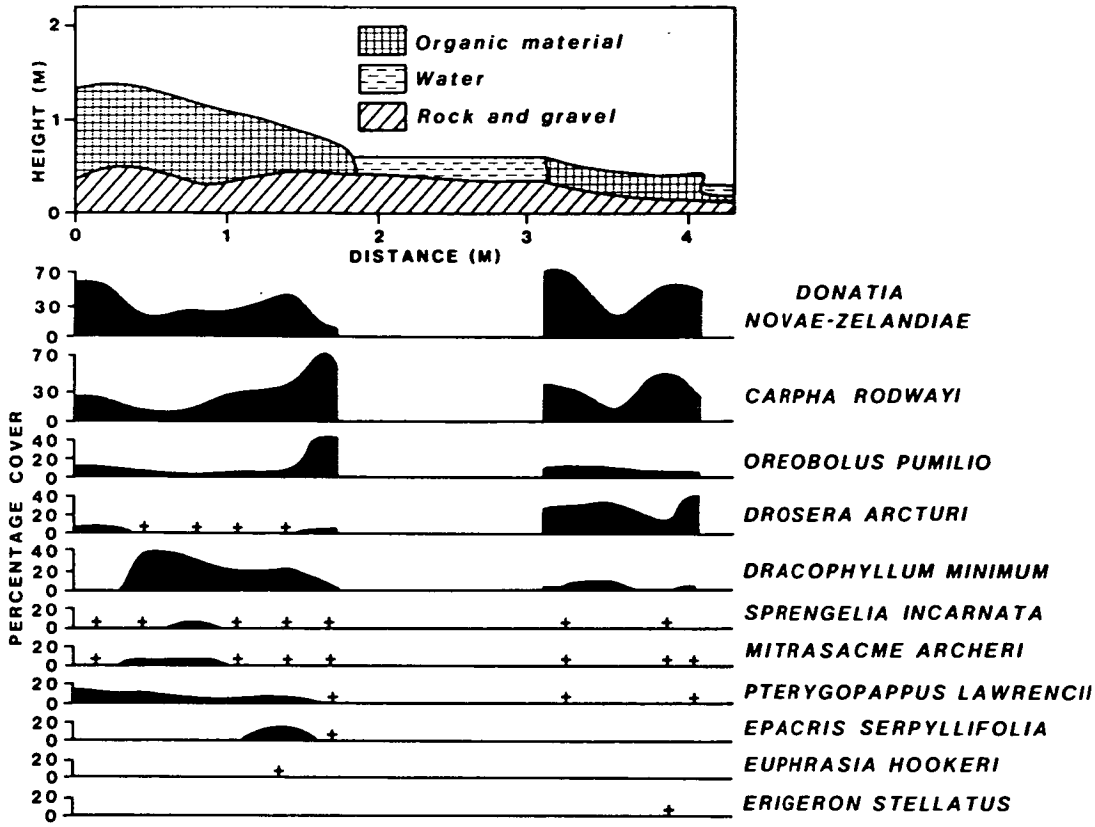

Fig. 2. The cover of higher plant species across the upper part of the transect K-L (Fig. 1). + = present to an insufficient degree to show to scale.

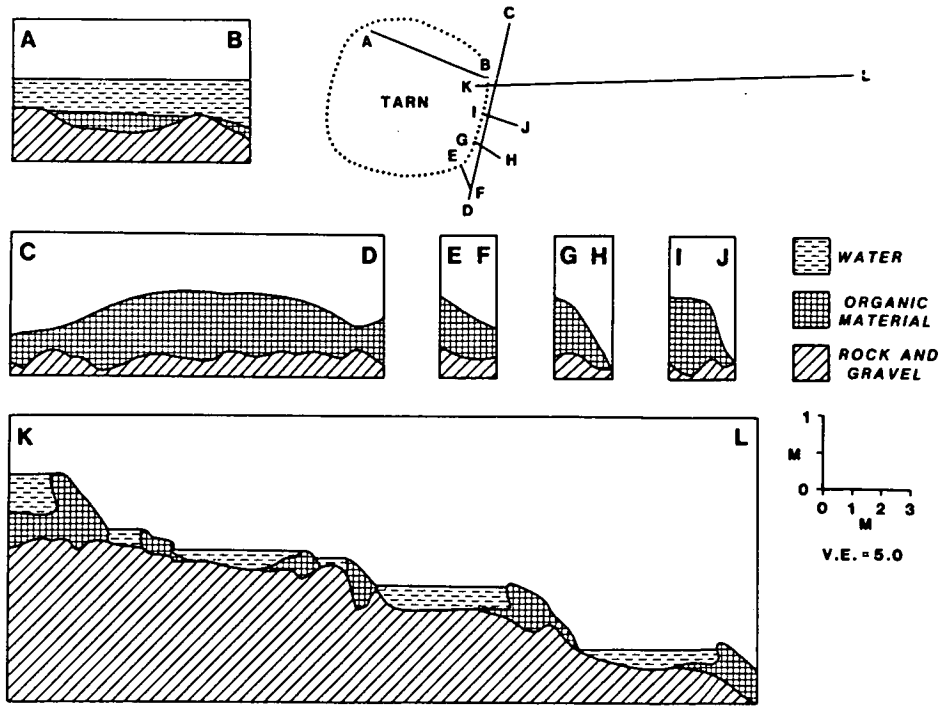

Fig. 3. Transects through string and flark features showing the surface and underlying topography and water levels when full.

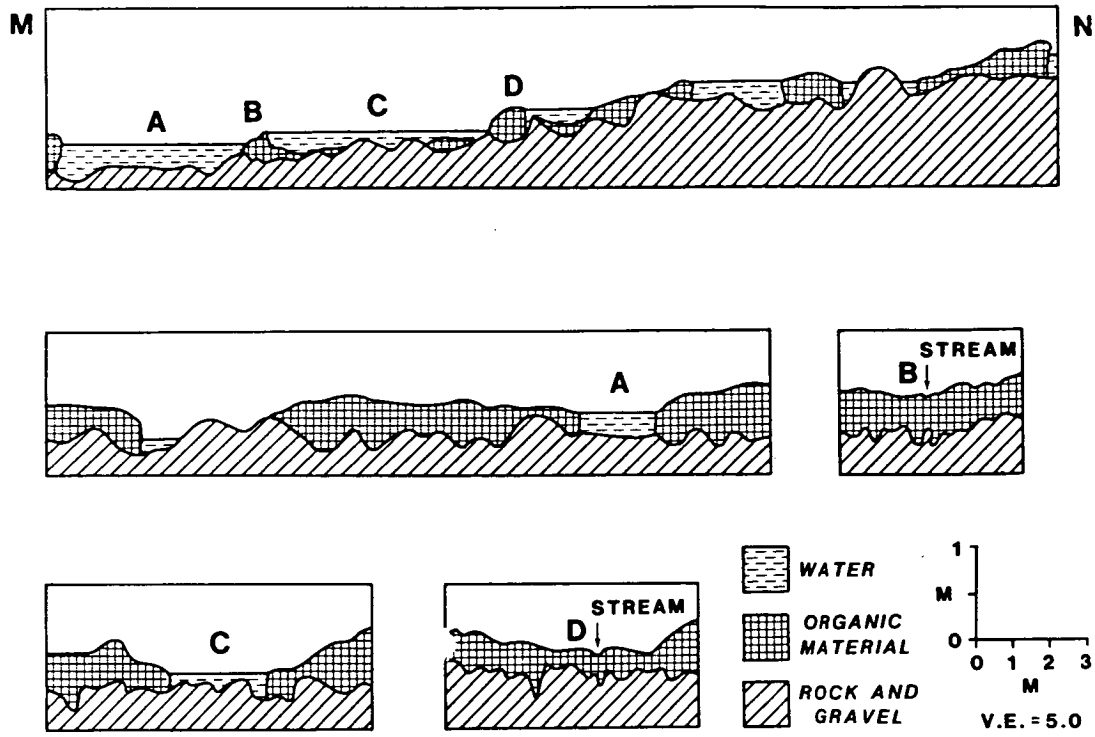

Fig. 4. Transects along (above) and across (A, B, C, D below) a stream line through string and flark topography.

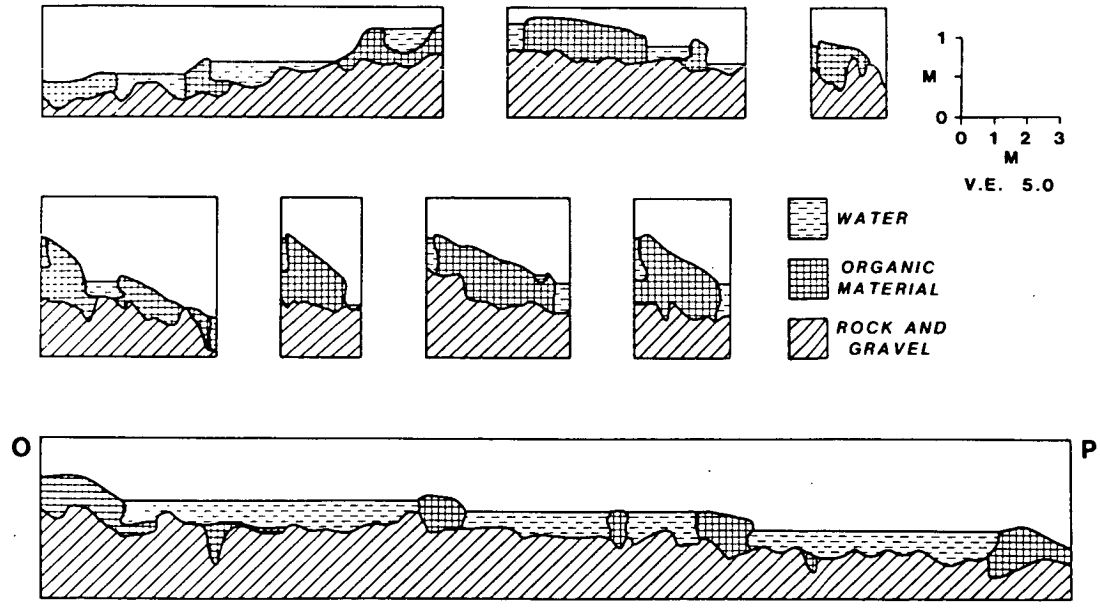

Fig. 5. Transects through string and flark features showing the surface and underlying topography and water levels when full. Note the pond in peat in the upper left-hand diagram and the shape of the inner downstream walls in the bottom section which runs west to east from left to right.

seldom vertical. In most cases they are apparently undercut at the base, the undercutting being greatest where the water is deepest and usually occurring below the live roots of the surface mat of vegetation. Substantial localized cave formation occurs in those places at the upslope end of the flark pools where the throughflow of water is concentrated. Pools with relatively long fetches available to the prevailing westerly winds exhibit a different shape on their leeward edges (Fig. 5). Here they are gently sloped with peat extending well above the water outlet level. Several of the uppermost flark ponds back on to boulder streams rather than being surrounded by peat walls, and in some cases rocks are incorporated in the surface of peat walls, although the general tendency is for them to be overgrown by the bolster species.

The peat walls are up to 1.15 m deep and overlie dolerite boulders or dolerite gravel. In most of the dam cross-sections in Figures 4–6 a peak in the underlying surface can be identified downslope of the current pool/dam boundary. The vegetated slope of the dam wall can be up to 90° from horizontal. The steepest parts of the downslope walls are convex, whereas the side walls are often concave (Fig. 3). The steepest measured overall dam slope from tarn to tarn was 30°.

The remains of old dams, with the shoot structure of the bolster plants still visible in the peat, were found beneath the water of three flark ponds. In two ponds the rooted remains of upright shrubs were found beneath the water. The loose organic detritus that covered the mineral floor of some ponds accumulated most near their centre (Fig. 3). Some of the smallest ponds had developed in the bolster heath peat (e.g. Fig. 5).

The stream cross-sections in Figure 4 illustrate a partial independence of surface flow and underlying topography. In most cases examined the surface outlet was not located above the lowest channel in the mineral substratum.

The tallest dams were those where surface flow was absent or weak, even after heavy rain. The pools along lines of persistent surface flow (e.g. Fig. 4) had relatively low dams and a high incidence of recent breaching. Most pools along lines of persistent surface flow have their outlet level controlled by a rock that is exposed or nearly exposed at the base of a usually narrow, steep-sided and often sinuous channel. Breaching is relatively widespread within the study area (Fig. 1) where it takes place through tunnels in the amorphous peat below the live plant roots. These tunnels run from the point of greatest depth at the downslope wall of the upper tarn to the point of greatest throughflow at the back wall of the lower tarn, their bases being usually partly on the underlying rock surface. In some cases the roofs of the tunnels are sufficiently near the surface to collapse under the weight of people or the larger marsupials that inhabit the area.

A model of formation

The above observations are most simply explained by a largely biological process whereby the bolster or other compact species block near surface drainage in boulder streams, raise themselves into dams and after considerable vertical growth the backed up pool empties by tunnelling through the amorphous peat below plant roots (Fig. 6).

The Newdegate Pass string and flark features have formed on the surface of a boulder stream. This and other boulder streams have stepped surfaces where smaller boulders accumulate behind larger ones. Yellow-brown clay is sometimes intermixed with the boulders and usually lies beneath them. The boulder streams occupy the valleys and

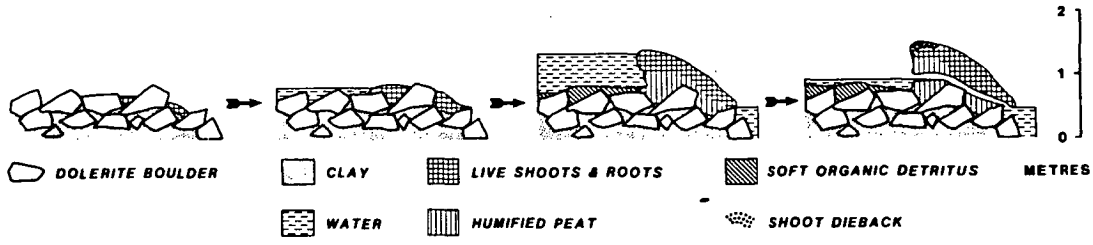

Fig. 6. A model of development and breaching of bolster dams.

slopes, thus receiving considerable drainage from above. This drainage flows on the surface of the underlying clay, moving rapidly in incised subterranean streams on steep slopes and in gentle subterranean sheet flow where slopes are shallow. Where the clay is close to the surface of the boulder stream plant growth becomes established. Where drainage is good gymnosperms or proteaceous and epacridaceous shrubs become established. Where flushing is fast *Astelia alpina* establishes and where flushing is slow the bolster species, including *Carpha rodwayi*, establish. The bolster community extends both vertically and laterally, its vertical growth being fastest in situations where moisture is constant but prolonged inundation absent. Thus, where there are no strong streams, the bolster plants block lines of maximum flow and cause conditions suitable for their own lateral growth. Conditions for growth of the bolster community are equal on all parts of a dam surface, because any faster growing parts would soon cease to receive enough percolated moisture to maintain growth superior to that on lower parts of the dam. The upward and outward growth of the bolster community may envelop other shrub species, some of which survive with their foliage on the bolster surface. The areas inundated by the bolster dams are soon bereft of non-aquatic higher plants. Little or no organic material accumulates in the oligotrophic waters, whereas the bolster community grows on a soil of its own making with a self-regulated water supply and aeration.

As the dam walls grow they assume a concave inner shape. This shape may be partly due to the restriction of active plant growth to the upper part of the wall where inundation is infrequent. However, it is probably largely due to erosion of the lower part of the wall where the peat is most humified and least bound with live plant roots, and thus least resistant to disruption and removal through wave action or other water movement (Ivanov, 1981). The seepage of water through peat declines drastically with increasing humification (Ivanov, 1981, p. 78). There is generally a sharp break in the dams between peat still occupied by live roots at 20–30 cm depth and peat without roots below these depths, creating a situation where fast flow is likely to occur immediately above very slow flow through the interstitial network. It is therefore not surprising that tunnels form, especially where seepage through the dams tends to concentrate as it drips into the flark below. The tunnels that break through a dam tend to begin in the deepest part of the dam, and occur most frequently along lines of rapid flow, suggesting that hydrostatic pressure may play a part in their genesis. The tendency for rocks to form part of the floor of tunnels and also to be the floor of outlets for many of the pools along persistent streams suggests that they form a base for any rapid erosion. Pools will only persist along rapidly flowing surface drainage lines where a rock forms the base for tunnel erosion above the minimum level of the depression to the rear. The breaching of one dam may lead to the successive breaching of those downstream as a result of increased peak flows.

Any complete or partial breach of a dam that results in a reduction of flark pond water levels by 15 cm or more is associated with extensive necrosis of those parts of the dam which thereby become ombrotrophic peat. Where the dams have enveloped still surviving non-bolster shrubs, their growth is enhanced with improved drainage and they eventually become dominant. However, non-bolster shrub species are very infrequent invaders of decaying dams. The peat of such dams appears to oxidize until a level in equilibrium with the new water table is established, and much of the dam can be eroded away by water flowing through enlarged, collapsed tunnel breaches. Such erosion continues until the underlying rock is exposed. The formation of new dams is initiated in the middle of the drained flarks where *Carpha rodwayi, Scirpus productus* and, later, the bolster species make best growth.

There may be an upper limit to dam height, controlled by the impact of hydrostatic pressure on humified peat, that ensures a changing landscape at Newdegate Pass. Peat accumulations of 1.15 m suggest a long history given the 3–8 mm per annum growth rate established for bolster species (Bliss & Mark, 1974; Gibson, unpublished data) and the compression and losses involved in peat formation (Tallis, 1983). Data reviewed by Tallis (1983) and the results of Andrews *et al.* (1975) suggest that the rate of peat formation in the alpine environment of Newdegate Pass could be expected to be less than two cm per century. Thus, there is a strong possibility that the deepest peats in the dams (1.15 m) could have begun forming in the early Holocene.

General discussion

The strongest evidence for the validity of the cyclic model of development of the bolster heath string fens at Mt. Field postulated above is the presence of each stage of development and disintegration in the present vegetation. The model is being further tested by the monitoring of changes in permanent photographic quadrats laid out in the summer of 1983. Poor preservation of the pollen of the bolster species and the high degree of floristic similarity between the vegetation colonizing newly drained flarks and that covering well-established dams suggested to us that a palynological approach to the problem would be unproductive. We have suggested that some of the taller dams may date from the early Holocene. The conservative calculation of a temperature drop of 5.5 °C during the Last Glacial compared to the present (Kiernan, 1983) would place Newdegate Pass above the snow line, and re-establishment of bolster plants may not have occurred until the deglaciation of Mt. Field approximately 10 000 yr ago (Macphail & Peterson, 1975).

Thus, although the system is dynamic and is partly independent of the underlying topography, any major short-term change is necessarily degradational, the rapid homeostatic mechanisms found in the case of the staircase ponds of Ives (1941) being distinctly absent. Fire, caused by man, and trampling has led to the drainage of flark ponds at Newdegate Pass and elsewhere on Mt. Field. However, most drained flark ponds in the study area show no evidence of having been caused by human interference.

Our model of cyclic change partly supports both the initial hypotheses. Tall shrub invasion was not observed to result from the drainage of flark ponds, and the string and flark features are not a mere accentuation of a pre-existent topography. Nevertheless, shrubs can occasionally replace bolster heath on sites to which bolster heath can only return after an intermission as a pool, and the slight stepping in the underlying boulder stream exerts some influence on the location of features.

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Accepted 25.6.1984.

New Zealand Journal of Botany, 1985, Vol. 23: 549-566
0028-825X/85/2304-0549$2.50/0

A comparison of the cushion plant communities of New Zealand and Tasmania

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Abstract Communities dominated by species of cushion plants are widespread in the alpine and subalpine zones of New Zealand and Tasmania. In New Zealand this vegetation type contains six major associations. These are described as alpine herbmoor, cushion bog, high alpine cushion moor, alpine cushion herbfield, and rock and river shingle cushion communities, their distributions being closely related to particular geomorphic environments. In Tasmania there are four major associations. These are described as *Abrotanella* cushion heath, high mountain cushion heath, mosaic cushion heath, and *Donatia* cushion heath, their distributions being most closely related to altitude, precipitation, and rock type. Of the six New Zealand cushion associations, herbmoor and cushion bog have the highest proportion of species also occurring in Tasmania. The differences between Tasmanian and New Zealand cushion associations largely result from differences in topography. Tasmania lacks the rock and river shingle environments, completely lacks the high alpine zone (Wardle 1964), and lacks the extensive alpine and subalpine snow tussock grasslands common in New Zealand.

Keywords bolster; cushion; Tasmania; New Zealand; alpine; bog; herbmoor; shingle; rock; cushion moor; herbfield; cushion heath

Received 28 January 1985; accepted 22 May 1985

INTRODUCTION

Cushion plants are an unusual life-form locally common in the alpine and subalpine vegetation of Tasmania and New Zealand as well as South America and the subantarctic islands (Godley 1978, Taylor 1955, Pisano 1983). They are chamaephytes or hemicryptophytes with closely packed shoots and very short internodes, forming compact, often hard, cushions to more than three metres in diameter. Cushion plants are recorded from over thirty families and from environments which range from the high dry tundra of Peru, to bogs, and to river shingle (Hodge 1946, Cockayne 1958). They also occur in alpine areas of the northern hemisphere but are not as well developed there as in the southern hemisphere (Bliss 1971, 1979).

Several hypotheses have been put forward to explain the evolution of this life-form. These variously explain the cushion habit as a response to intense radiation, temperature, physical and physiological drought, low soil fertility, and wind action, these factors acting in isolation or conjunction (Ruthsatz 1979; Bliss 1956, 1971; Billings 1974; Hedberg & Hedberg 1979; Tiffney 1972; Spomer 1964).

The aims of this paper are to define the associations in which cushion plants dominate in the South Island of New Zealand and Tasmania, to undertake a comparison of floristic composition between these associations and to describe briefly the environments in which these associations occur. In addition a comparison of the distributional patterns of the shared cushion species is presented.

The term bolster has been used to describe the hard compact nature of the major cushion species in Tasmania (e.g., *Donatia novae-zelandiae**, *Abrotanella forsteroides* (Hook f.) Benth., *Dracophyllum minimum*, *Phyllachne colensoi*, and *Pterygopappus lawrencii*). In New Zealand such species as *Haastia pulvinaris*, *Raoulia bryoides*, and *Raoulia eximia*

*Nomenclature follows Allan (1961), Moore & Edgar (1970), Healy & Edgar (1980), and Mark & Adams (1979) in New Zealand and Curtis (1963, 1967), Curtis & Morris (1975), and Costin et al. (1979) in Tasmania, except where otherwise indicated. Vegetation terminology follows Wardle (1964) for New Zealand and Kirkpatrick (1983) for Tasmania.

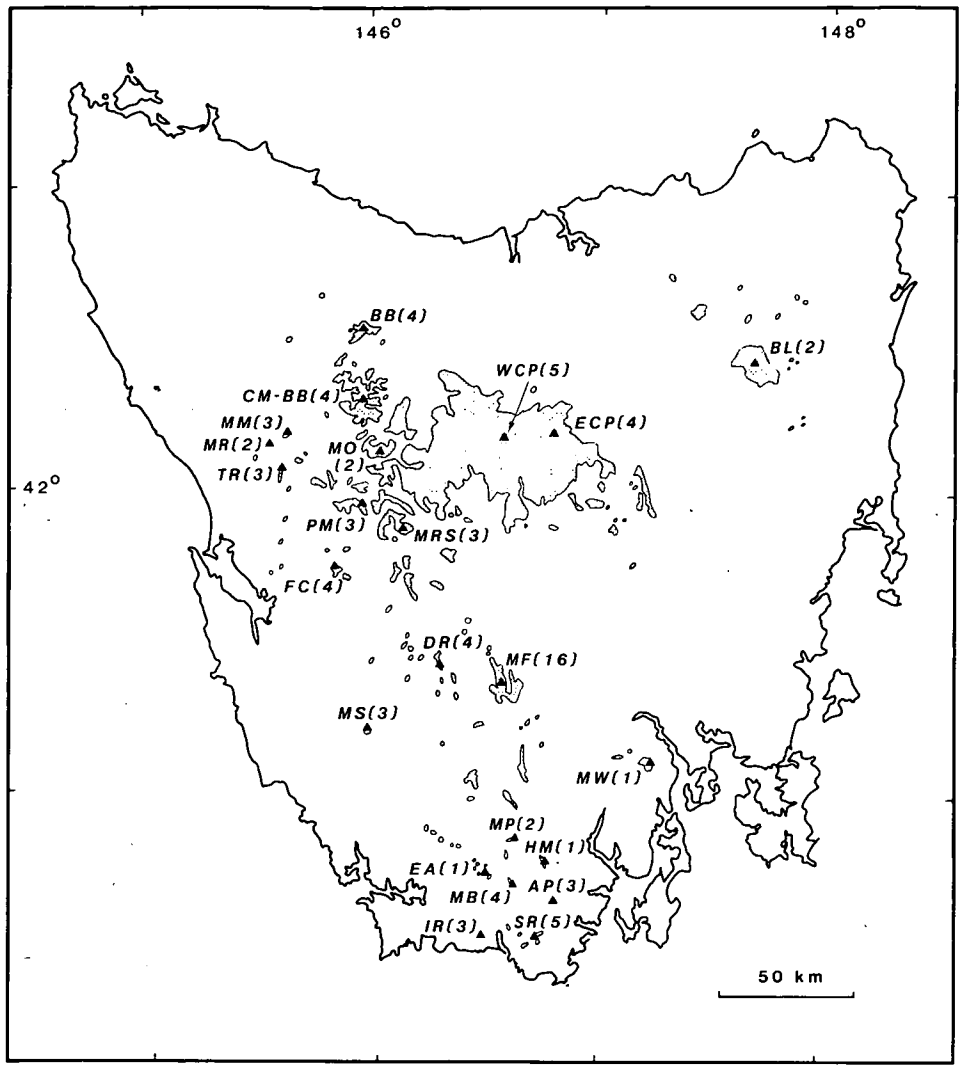

Fig. 1 Map of Tasmania showing land above 1000 m, the 23 mountain areas visited, and the number of quadrats sampled. Mountains listed from south to north — SR, Southern Ranges; IR, Ironbound Range; MB, Mount Bobs; AP, Adamsons Peak; EA, Eastern Arthur Range; HM, Hartz Mountains; MP, Mount Picton; MW, Mt Wellington; MS, Mount Sprent, MF, Mount Field; DR, Denison Range; FC, Frenchmans Cap; MRS, Mount Rufus; PM, Pyramid Mountain; TR, Tyndall Range; MR, Mount Read; MO, Mount Ossa; WCP, Western Central Plateau; ECP, Eastern Central Plateau; MM, Mount Murchison; CM-BB, Cradle Mountain-Barn Bluff; BB, Black Bluff; BL, Ben Lomond.

have the same physiognomy but have been generally referred to as cushion plants, a term which includes the softer mat-cushions. In this paper the term cushion plant is used in its widest sense, to include both soft mat and bolster forms.

Mountain environments of the study areas

Tasmania, lying between 40°30′S and 45°45′S, is the most mountainous area in Australia (Fig. 1). In the west, mountains reaching 750–1400 m altitude are formed from Precambrian metaquartzites. In the centre and east these Precambrian rocks are overlain by Triassic, Permian, and upper Carboniferous sediments, which are generally capped by Jurassic dolerites. The central and eastern mountains are mostly high (1000–1617 m) dolerite plateaus, which contrast markedly with the more rugged western peaks.

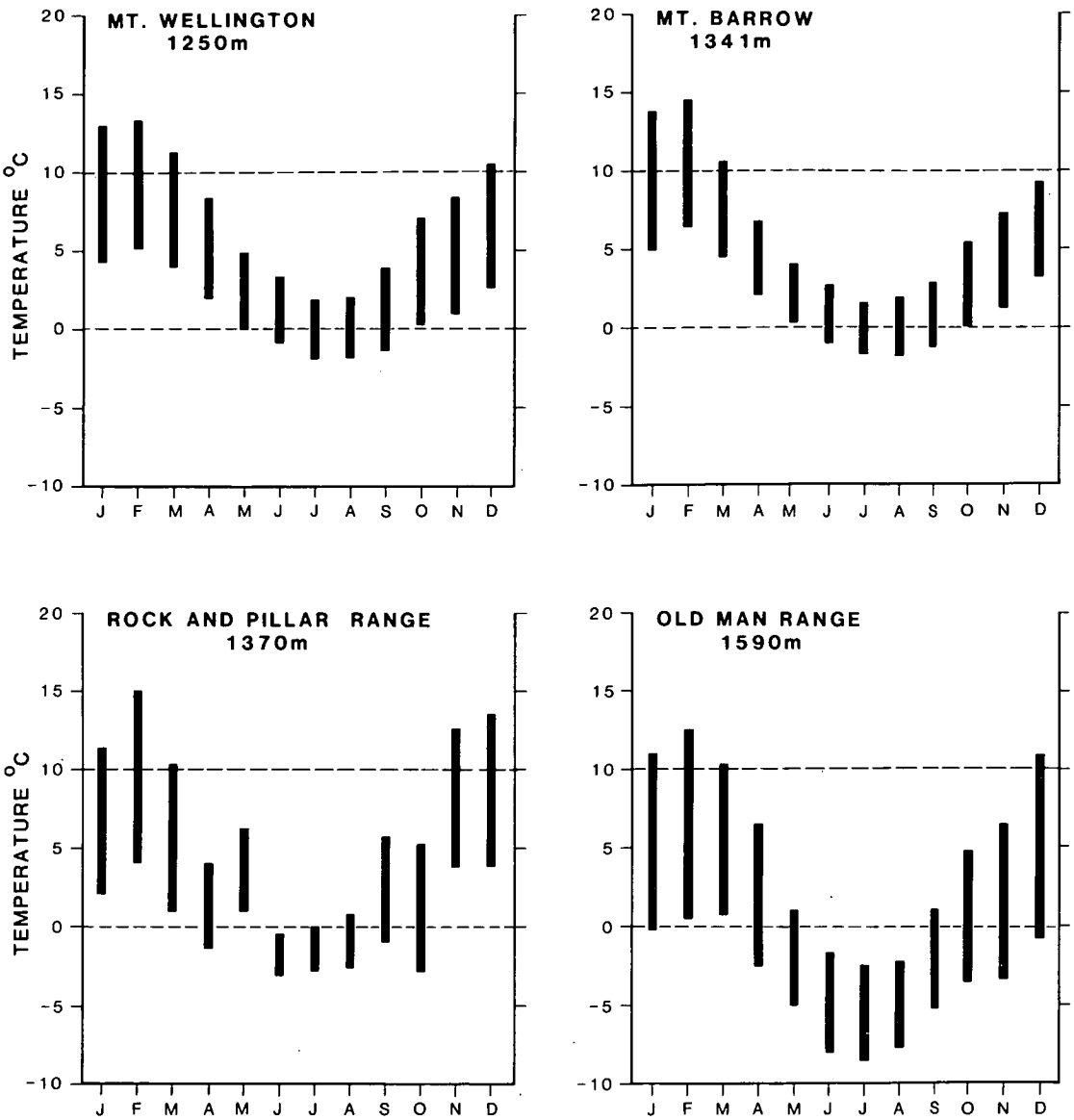

Fig. 2 Mean monthly maximum and minimum temperature data for Mt. Wellington amd Mt. Barrow, Tasmania; Rock and Pillar Range and Old Man Range, New Zealand (after Bureau of Meteorology 1975; Bliss & Mark 1974; Mark & Bliss 1970).

The prevailing westerly airflow causes a precipitation gradient from over 3600 mm in the Tyndall Range to less than 1000 mm on parts of the eastern Central Plateau. Tasmanian mountains generally lack a distinct tree-line (Kirkpatrick 1982, 1983). Available long-term climatic data indicate a more maritime climate than for the Australian alps (Kirkpatrick 1983, Fig. 2). Snow can fall at any time of the year while long periods of snow-lie, even in winter, are rare. The climatic tree-line varies from approximately 750 m in the southwest of the island to approximately 1400 m in the north-east (Kirkpatrick 1982).

The highly dissected glacial landscape of the South Island of New Zealand lies between 40–46°S (Fig. 3). The Southern Alps lie in the west along the still active Alpine Fault and range in height from 2000–3766 m. They largely consist of Mesozoic

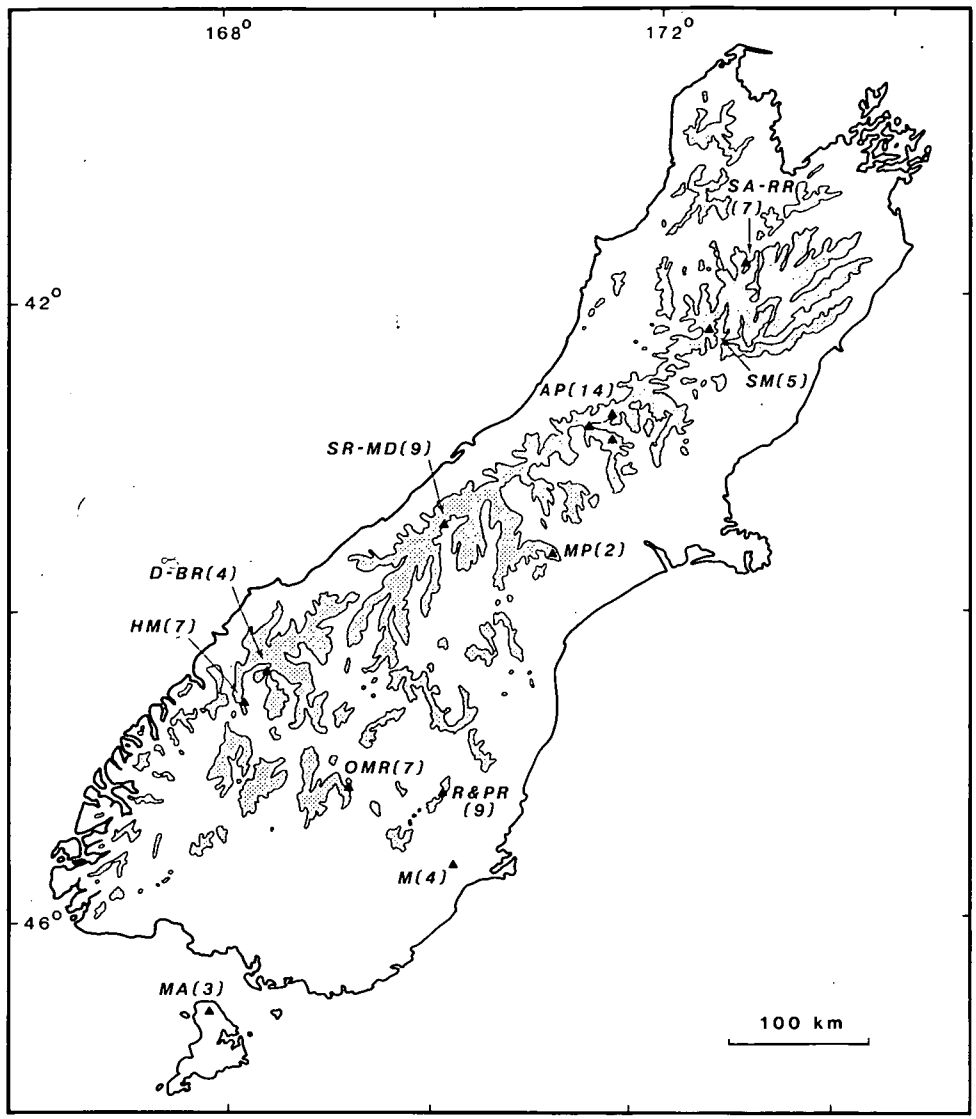

Fig. 3 Map of South Island, New Zealand showing land above 1000 m, the 11 mountain areas visited and the number of quadrats sampled. Mountains listed from south to north — MA, Mount Anglem; M, Maungatua; R&PR, Rock & Pillar Range; OMR, Old Man Range; HM, Humboldt Mountains; D-BR, Dart-Barrier Range; MP, Mount Peel; SR-MD, Sealy Range-Main Divide; AP, Arthur's Pass; SM, Spencer Mountains; SA-RR, St Arnold-Robert Ridge.

greywackes with a western band of late Mesozoic chloritic schists sweeping eastward, in Central Otago, between Lakes Hawea and Wakatipu to the coast. The generally flat topped mountains of this central Otago area range in maximum height from 1300–2400 m. A further band of metamorphosed Ordovician sediments, wrenched apart by several hundred kilometres of movement along the Alpine Fault, form the mountains of Fiordland and western Nelson (1500–2000 m). Extensive glacial outwash plains occur to the east of the Canterbury section of the alps (New Zealand Geological Survey 1972). The summer snow-line lies at about 2200m, varying somewhat with latitude and aspect (Cockayne 1958).

There is a strong precipitation gradient from west to east, the annual amount ranging from over 10 000 mm along the divide to 1000–2100 mm on

the central Otago mountains (Griffiths & McSaveney 1983, Mark & Bliss 1970, Bliss & Mark 1974). Much precipitation falls as snow in winter when extended periods of snowlie are common. The tree limit varies from 900 m in Fiordland (46°S) to 1200 m at latitude 41°S, and in the more continental island regions of the South Island the tree-line rises to 1500 m (Wardle 1973). Aspect may further influence the altitude of the tree-line. In the central Southern Alps and central Otago, the absence of forest vegetation is considered to be a result of burning first by Maoris, and subsequently by Europeans (Molloy et al. 1963). Temperature data from central Otago indicate a colder alpine environment than recorded for Tasmania (Fig. 2). Whereas it is common for the soil to freeze in central Otago, soil freezing rarely occurs in Tasmania. Central Otago mountains have a frost free period of only a few weeks whereas at Mt. Field in south central Tasmania this period may extend over several months in summer (Mark & Bliss 1970, Gibson unpublished data).

METHODS

During the summer of 1983–84, data were collected from 70 ten by ten metre quadrats in which cushion plants constituted most of the cover from 11 mountain areas in the South Island, and Stewart Island, New Zealand (Fig. 3). Similar data from 82 ten by ten metre quadrats were collected from 23 Tasmanian mountains between 1973 and 1984 (Fig. 1). In each quadrat presence/absence data were collected for all vascular plants and observations on the vegetation structure and site conditions were recorded.

The Tasmanian cushion communities have been thoroughly sampled. Time and logistics did not allow as complete a sampling of South Island, New Zealand cushion communities. In particular, the cushion species *Myosotis uniflora, M. pulvinaris, Raoulia mammillaris, R. youngii*, and *Chionohebe myosotoides* (Ashwin) Briggs et Ehrendorfer did not occur in our data set. The data sets were separately classified using the polythetic divisive classification procedure, TWINSPAN, which produces simple dichotomies (Hill 1979). The levels of division used were determined subjectively by the coherence of the ecological groups obtained. The data sets were separately ordinated using detrended correspondence analysis (Hill & Gauch 1980).

Distributional information for selected New Zealand and Tasmanian species was compiled from the Botany Division, DSIR (CHR) and Otago (OTA) herbaria, the literature, and the data of the authors. This information was plotted on a 10 km square grid based on NZMS 262 1:250 000 in New Zealand and the Tasmanian 1:100 000 sheets.

RESULTS AND DISCUSSION

A total of 196 and 164 taxa were recorded in New Zealand and Tasmania respectively. Because of some determination difficulties, it was necessary to lump some species (Table 1 and 2).

Numerical analysis of New Zealand data

The classification produced by TWINSPAN delimited six ecologically recognisable groups (Fig. 4, Table 1). Types 1 and 2 are characterised by the dominance of *Donatia novae-zelandiae* and *Oreobolus pectinatus*. Type 1 is restricted to Stewart Island and type 2 occurs widely in the South Island. Quadrats containing *Dracophyllum muscoides* from the central Otago mountains form type 3, where as type 4 generally contains *Phyllachne colensoi*- and/or *Celmisia sessiliflora*-dominated vegetation, or occasionally *Colobanthus* spp. may dominate. A small group of species-poor, high altitude scree quadrats form type 5, and are characterised by the dominance of *Haastia pulvinaris*. Type 6 encompasses the vegetation of the unconsolidated gravels of the braided river valleys, dominated by *Raoulia tenuicaulis*. This environment is referred to as river shingle. The vegetation of the river shingle covers a seral series, groupings being dependent on species richness (mean of type 6A — 7 spp.; type 6C — 10 spp.; type 6B — 25 spp.). The ordered table (Table 1), with minor species reallocation, clearly shows the distinctive groups of taxa in the classification.

The ordination (Fig. 4) shows as extremes along the first axis, bog communities (types 1 and 2) and river shingle communities (type 6); along the second axis, high alpine cushion moor (type 3) and rock community (type 5). There is a strong relationship between the classificatory groups and the substrates occupied by the quadrats in the groups. There is no simple relationship between the position of the quadrats on the two axes and any single environmental variable, although soil moisture and substrate stability gradients are related strongly to the differences between the communities as shown by the ordination (cf. Belsky & del Moral 1982).

The New Zealand associations and their environmental correlates

Five of the six New Zealand associations revealed by TWINSPAN are illustrated in Fig. 5. These associations are described as:

1. Alpine herbmoor: (not illustrated) Cockayne (1958) describes herbmoor as a peat-forming formation intermediate in character between wet herbfield and bog, which is distinguished by the absence of tall plants and the abundance of turf-forming, prostrate, and cushion species. This association was

Table 1 Classification of New Zealand quadrats and species. Species shown occur with a frequency of 20 per cent or more in at least one group. (▲ indicates the cushion lifeform, and † indicates introduced species).

Species	Classificatory groups 1	2	3	4	5	6	Species groups
Astelia linearis	100.0	–	–	–	–	–	
Celmisia aff. *du-rietzii*	100.0	–	–	–	–	–	
Bulbinella gibbsii	100.0	–	–	–	–	–	
▲*Dracophyllum politum*	100.0	8.3	–	–	–	–	
▲*Raoulia goyenii*	66.7	–	–	–	–	–	A
Halocarpus biformis (Hook.) Quinn	66.7	–	–	–	–	–	
Olearia colensoi	33.3	–	–	–	–	–	
Microlaena thomsonii	33.3	–	–	–	–	–	
Gleichenia dicarpa R. Br.	33.3	–	–	–	–	–	
Schoenus pauciflorus	33.3	4.1	–	–	–	–	
Oreobolus strictus	66.7	20.8	–	–	–	–	
▲*Gaimardia setacea*	–	45.8	–	–	–	–	
Dracophyllum prostratum	–	37.5	–	5.6	–	–	
Halocarpus bidwillii (Hook. f. ex Kirk) Quinn	–	20.8	–	–	–	–	
Cyathodes empetrifolia	33.3	8.3	–	–	–	–	
▲*Centrolepis ciliata*	–	25.0	–	–	–	–	
Drosera arcturi	–	91.7	–	–	–	–	
▲*Donatia novae-zelandiae*	100.0	75.0	–	–	–	–	B
Lepidothamnus laxifolius (Hook. f.) Quinn	–	20.8	–	–	–	–	
Cyathodes pumilia‡	–	54.2	–	5.6	–	–	
Pentachondra pumila	66.7	75.0	–	11.1	–	–	
▲*Oreobolus pectinatus*	33.3	100.0	–	16.7	–	–	
Carex spp.	–	41.7	–	5.6	–	–	
Carpha alpina	100.0	75.0	7.1	11.1	–	–	
Hebe pauciramosa	66.7	12.5	–	–	–	–	
Celmisia glandulosa	–	37.5	–	11.1	–	–	
Senecio bellidioides	–	25.0	7.1	11.1	–	–	
Senecio lyallii	66.7	–	–	5.7	–	–	
Dracophyllum uniflorum	–	29.2	–	5.7	33.3	–	
Coprosma pumila	66.7	37.5	7.1	33.3	–	–	C
Epilobium spp.	33.3	–	7.1	–	–	–	
Chionochloa spp.	33.3	50.0	–	55.7	–	–	
Dracophyllum pronum	–	8.3	–	16.7	33.3	–	
Gentiana spp.	–	58.3	57.1	72.2	–	16.7	
▲*Drapetes lyallii*	100.0	–	21.4	22.2	–	–	
▲*Celmisia argentea*	33.3	12.5	50.0	–	–	–	D
Lycopodium fastigiatum	–	33.3	57.1	44.4	–	–	
Plantago novae-zelandiae	33.3	12.5	14.3	22.2	–	33.3	
Marsippospermum gracile	–	12.5	–	55.6	–	–	
Gaultheria depressa	33.3	8.3	–	66.7	–	–	
▲*Celmisia sessiliflora*	–	8.3	–	72.2	–	–	
Celmisia haastii	–	4.2	–	38.9	–	–	
▲*Phyllachne colensoi*	–	16.7	42.9	88.9	–	–	
Poa colensoi	–	29.2	92.9	88.9	33.3	33.3	
Celmisia laricifolia	–	12.5	57.1	22.2	–	–	
Agrostis subulata	–	8.3	14.3	22.2	–	33.3	E
Luzula traversii	–	–	–	5.6	–	33.3	
Luzula rufa	–	–	14.3	33.3	–	16.7	
▲*Chionohebe ciliolata* (Hook. f.) Briggs et Ehrendorfer	–	–	–	22.2	–	–	
Euphrasia revoluta	–	4.2	–	22.2	–	–	
Drapetes dieffenbachii	–	–	–	38.9	–	–	
Raoulia grandiflora	–	4.2	50.0	77.8	–	16.7	

Table 1 cont.

Species	Classificatory groups 1	2	3	4	5	6	Species groups
Anisotome flexuosa	–	–	28.6	44.4	–	–	
Hebe ciliolata	–	–	21.4	22.2	–	–	
Craspedia lanata	–	–	35.7	–	–	–	
▲*Raoulia hectoria*	–	–	100.0	–	–	33.3	
Poa buchananii	–	–	37.5	5.7	–	–	
▲*Phyllachne rubra*	–	–	87.5	–	–	–	
Luzula pumila	–	4.2	100.0	16.7	–	50.0	
▲*Hectorella caespitosa*	–	–	71.4	11.1	–	–	F
Drapetes villosus	–	–	42.7	11.1	–	–	
▲*Dracophyllum muscoides*	–	–	100.0	5.6	–	–	
▲*Colobanthus* spp.	–	–	50.0	16.7	33.3	33.3	
Celmisia viscosa	–	–	50.0	22.2	–	–	
Anisotome imbricata var. *imbricata*	–	–	57.1	–	–	–	
Abrotanella aff. *inconspicua*	–	–	57.1	5.7	–	–	
▲*Raoulia bryoides*	–	–	–	5.7	33.3	–	
Poa novae-zelandiae	–	–	–	–	33.3	–	
▲*Raoulia eximia*	–	–	–	–	33.3	–	G
Chionochloa australis	–	–	–	5.7	66.7	–	
Epilobium rubromarginatum	–	–	–	–	66.7	–	
▲*Haastia pulvinaris*	–	–	–	11.0	100.0	–	
Wahlenbergia albomarginata	–	–	–	–	–	33.3	
▲*Raoulia glabra*	–	–	–	–	–	33.3	
▲*Raoulia australis*	–	–	–	–	–	33.3	
†*Hieracium praealtum*	–	–	–	–	–	33.3	
Parahebe decora	–	–	–	–	–	50.0	H
Epilobium melanocaulon	–	–	–	–	–	50.0	
Stellaria gracilenta	–	–	–	–	–	50.0	
†*Agrostis tenuis*	–	8.7	–	–	–	66.7	
▲*Raoulia tenuicaulis*	–	–	–	–	–	100.0	

‡This species is probably conspecific with the Tasmanian *Cyathodes dealbata.*
Cushion species with frequencies of less than 20%:
Group 2 *Oreobolus impar*
Group 3 *Chionohebe thomsonii*
Group 4 *Oreobolus impar, Raoulia hookeri; Raoulia subsericea, Chionohebe pulvinaris*
Group 6 *Oreobolus impar*

only recorded from Mt. Anglem on Stewart Island (type 1) where it forms a closed community with *Dracophyllum politum, Chionochloa pungens*, and *Donatia novae-zelandiae* as the dominant species and has been described in some detail by Wells & Mark (1966). This community is much more extensive on mountains south of Paterson's Inlet which were not visited in this survey (H. D. Wilson pers. comm.). It may be that the subantarctic climate of these areas reduces competition from snow tussock grassland and thus allows herbmoor to develop (Cockayne 1958), or alternatively local edaphic factors may control the vegetation patterns. This community is most similar physiognomically to the mosaic cushion heaths of Tasmania. It is typified by species group A (Table 1).

2. Cushion bogs: (Fig. 5a) Quadrats in type 2 are Cockayne's (1958) classic cushion bogs, which are generally subalpine or alpine, occupying small areas which are often surrounded by snow tussock grassland (*Chionochloa* spp.). These closed bogs are dominated by *Donatia novae-zelandiae* and/or *Oreobolus pectinatus.* Of the New Zealand communities, cushion bogs and herbmoor are floristically the most similar to the Tasmanian alpine vegetation (Table 3). Cushion bogs are typified by species group B and occur widely in the South Island, especially in the west and south (Table 1). Dobson (1979) suggested that cushion bogs form on oligotrophic sites where the mean annual temperature is less than 6°C. This community extends to sea level on the highly maritime Awarua Plains, near Invercargill; the climate here reducing the

Table 2 Classification of Tasmanian quadrats and species. Species shown occur with a frequency of 20 per cent or more in at least one group. (▲ indicates the cushion lifeform.)

Species	Classificatory groups 5	4	3	2	1	Species groups
Bauera rubioides	30.4	12.5	5.6	–	–	
Dracophyllum milliganii	56.5	25.0	16.7	–	–	
Isophysis tasmanica	56.5	12.5	11.1	–	–	
Microlaena tasmanica	39.1	25.0	–	–	–	
Actinotus moorei	21.7	62.5	–	–	–	
Anemone crassifolia	13.0	25.0	5.6	–	–	
Archeria comberi	–	37.5	–	–	–	A
Archeria hirtella	–	25.0	–	–	–	
Forstera bellidifolia	26.0	25.0	–	–	–	
Diplaspis cordifolia	34.8	37.5	16.7	–	–	
Euphrasia hookeri	21.7	12.5	22.2	5.0	–	
Milligania spp.	26.1	12.5	27.8	–	–	
Sprengelia incarnata	87.0	75.0	83.3	5.0	15.4	
▲*Donatia novae-zelandiae*	82.6	100.0	94.4	20.0	–	
Drosera arcturi	87.0	100.0	94.4	40.0	53.9	
▲*Gaimardia* spp.	17.4	12.5	38.9	5.0	–	
Campynema lineare	8.7	37.5	11.1	5.0	–	
Diselma archeri	13.0	50.0	–	5.0	–	B
Tasmannia lanceolata (Poir.) A.C. Sm.	4.4	75.0	11.1	10.0	–	
▲*Ewartia meridithae*	60.9	50.0	22.2	30.0	–	
Pentachondra pumila	60.9	100.0	27.8	40.0	–	
Actinotus suffocata	47.8	12.5	44.4	15.0	–	
Helichrysum milliganii	21.7	75.0	27.8	20.0	–	
Microcachrys tetragona	26.1	25.0	27.8	20.0	–	
Orites revoluta	8.7	62.5	16.7	15.0	7.7	
Abrotanella scapigera	13.0	12.5	5.6	25.0	–	
Exocarpos humifusus	–	25.0	–	5.0	–	
Helichrysum backhousii	13.0	25.0	11.1	40.0	–	
Olearia ledifolia	8.7	25.0	–	25.0	–	C
Richea sprengelioides	17.4	50.0	–	45.0	–	
Cyathodes dealbata	34.8	37.5	16.7	40.0	–	
Erigeron stellatus	52.2	87.5	55.6	55.0	–	
▲*Dracophyllum minimum*	8.7	12.5	61.1	45.0	–	
▲*Mitrasacme archeri*	39.1	12.5	83.3	55.0	–	
Schoenus calyptratus	–	–	16.7	35.0	–	
Celmisia saxifraga	4.4	37.5	44.4	80.0	7.7	
Euphrasia spp.	17.4	50.0	44.4	35.0	15.4	
Dichosciadium ranunculaceum	4.4	–	–	25.0	–	
Orites acicularis	–	12.5	11.1	40.0	–	
▲*Phyllachne colensoi*	–	–	–	70.0	–	
Uncinia compacta	4.4	25.0	–	65.0	7.7	D
Bellendena montana	–	37.5	5.6	20.0	7.7	
Danthonia pauciflora	4.4	37.5	38.9	40.0	23.1	
▲*Pterygopappus lawrencii*	4.4	12.5	72.2	40.0	61.6	
Senecio pectinatus	4.4	12.5	38.9	20.0	15.4	
Celmisia longifolia	13.0	62.5	–	35.0	38.5	
Astelia alpina	73.9	87.5	44.4	60.0	84.6	
▲*Carpha rodwayi*	78.3	75.0	94.4	60.0	76.9	
Lycopodium fastigiatum	39.1	62.5	5.6	35.0	30.8	
▲*Oreobolus pumilio*	95.7	100.0	88.9	45.0	69.2	E
Empodisma minus	87.0	62.5	22.2	15.0	84.6	
Epacris serpyllifolia	73.9	25.0	61.1	25.0	38.5	
Gleichenia alpina	30.4	12.5	5.6	–	15.4	
Richea scoparia	39.1	50.0	11.1	20.0	53.9	
Gentianella diemensis	17.4	37.5	27.8	35.0	38.5	
Luzula spp.	–	12.5	–	55.0	15.4	
Poa spp.	17.4	37.5	16.7	85.0	84.6	F

Table 2 cont.

Species	Classificatory groups 5	4	3	2	1	Species groups
Agrostis spp.	–	–	–	25.0	15.4	
▲*Abrotanella forsteroides*	13.0	–	44.4	15.0	100.0	
Danthonia spp.	–	12.5	5.6	30.0	30.8	
Rubus gunnianus	8.7	12.8	–	20.0	38.5	
Blechnum penna-marina	–	–	–	25.0	–	
Coprosma spp.	–	–	–	10.0	23.1	
Acaena novae-zelandiae	–	–	–	5.0	23.1	
Carex gaudichaudiana	–	–	–	5.0	30.8	
Richea acerosa	–	–	–	5.0	30.8	
Ranunculus spp.	–	–	–	10.0	30.8	
Hydrocotyle spp.	–	–	–	10.0	30.8	
Oreomyrrhis spp.	–	–	–	15.0	53.9	
Plantago gunnii	–	–	–	10.0	53.9	
Brachycome spp.	–	–	–	10.0	69.2	G
Gnaphalium spp.	–	–	–	15.0	69.2	
Helichrysum scorpioides	–	–	–	–	30.8	
Oreobolus distichus	–	–	–	–	30.8	
Velleia montana	–	–	–	–	30.8	
Microseris scapigera	–	–	–	–	30.8	
Pultenaea subumbellata	–	4.4	–	–	38.5	
Craspedia alpina	–	–	–	–	38.5	
Baeckea gunniana	–	13.4	–	–	38.5	
Epacris petrophila	–	–	–	–	46.2	
Asperula gunnii	–	–	–	–	46.2	
Restio australis	–	–	–	–	69.2	

Cushion species with frequencies of less than 20%:
Group 1 *Drapetes tasmanicus*
Group 2 *Oreobolus acutifolius* and/or *Oreobolus oxycarpus*
Group 3 *Oreobolus* spp.
Group 4 *Oreobolus* spp.
Group 5 *Oreobolus* spp., *Pimelea pygmaea*

vigour of species more typical of low altitude habitats (Cockayne 1958, Wardle 1964, Campbell 1983).

3. High alpine cushion moor: (Fig. 5b) This community (type 3) occurs exclusively on the central Otago mountains and is characterised by the occurrence of *Dracophyllum muscoides*. Mark & Bliss (1970) refer to this vegetation as cushion vegetation. However alpine cushion moor is considered a more definitive name, with moor being used to describe the short, flat nature of the vegetation. Cockayne (1958) has referred to this community as herbmoor. However, the non-accumulation of peat precludes this description. The cushion moor is characterised by species group F and covers a range of vegetation types, from areas of high wind exposure, where cover is less than 40%, to less exposed areas with cover values to 80% (Mark & Bliss 1970). Also included in this community is the more exposed stripe and hummock vegetation on non-active patterned ground, common in this region (Mark & Bliss 1970). High winds, short growing seasons, short frost free periods, long snow-lie, and rainfall around 1600 mm are characteristic of the climates of these mountains (Mark & Bliss 1970, Bliss & Mark 1974).

4. Alpine cushion herbfield: (Fig. 5c) Alpine cushion herbfield (type 4) is most widely distributed on alpine skeletal soils, generally on low to moderate slopes. It is best described as a subassociation within one of the snow tussock associations, but it does become a physiognomically distinct community in the high alpine zone (Cockayne 1958, Wilson 1976, Mark 1977). *Phyllachne colensoi* predominates through much of the South Island, occurring in low alpine snow tussock grassland on exposed areas or shallow soils, and extending upwards into more sheltered high alpine sites. Where *P. colensoi* is absent *Celmisia sessiliflora* generally becomes the dominant cushion species. Occasionally on high altitude, young moraine deposits, *Colobanthus* may be the dominant cushion plant in a community of

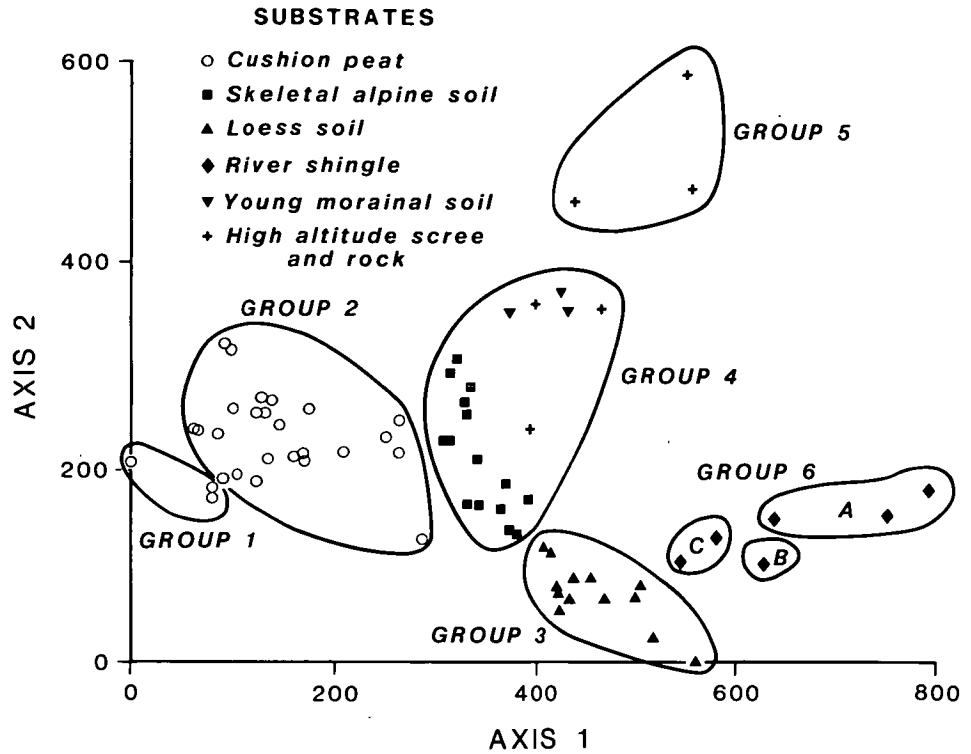

Fig. 4 Ordination of New Zealand data set showing classificatory groups and substrate of quadrats.

very low cover. Species group E characterises this community (Table 1). Distribution seems primarily dependent on exposure and soil depth. The ordination shows a gradation into the *Haastia pulvinaris* rock community. Although TWINSPAN splits the rock community between the cushion herbfield and the rock environment, this is considered to be a reflection of the sensitiveness of TWINSPAN to species richness. The species rich *H. pulvinaris* quadrats (with a mean of 13.5) were classified into type 4, whereas the species poor quadrats (mean = 4.7) were classified into type 5.

5. Rock cushion communities: (Fig. 5d) *Haastia pulvinaris, Raoulia eximia*, and *Raoulia bryoides* form the dominant species of rock cushion communities in drier north-east South Island. These and similar species are commonly called vegetable sheep; *Haastia pulvinaris*, the most robust, forms yellowish woolly cushions sometimes exceeding 3 m in diameter. They occur on the high altitude shattered rock and on the thinly mantled colluvial debris of these areas. Initially one of these species may be the only plant occurring on these barren sites, but the cushions eventually provide an environment suitable for the invasion of other species. Cover may increase to approximately 50 percent, with up to 20 or more species. At this stage community composition is similar to that of the alpine cushion herbfield, including such taxa as *Phyllachne colensoi, Marsippospermum gracile, Poa colensoi*, and *Celmisia* species. Species group G is highly faithful to this community.

6. River shingle cushion communities: (Fig. 5c) The geomorphologically active landscape of New Zealand produces braided river systems which are periodically subjected to flood and changing river beds. The cushion-mats *Raoulia tenuicaulis, R. australis*, and to a lesser degree *R. hookeri* are important in the early to mid-seral stages of the development from bare river shingle into the closed tussock grassland of the older terraces (Foweraker 1917, Calder 1961, Wardle 1972). Species group H is faithful to the river shingle environment (Table 1). This habitat is subject to both seasonal drought and periodic flooding. However, flooding and wind action are important in the sere, allowing accumulation of fines within the cushions, and thus helping in the development of a humus layer suitable for seedling germination during the later seral stages (Foweraker 1917).

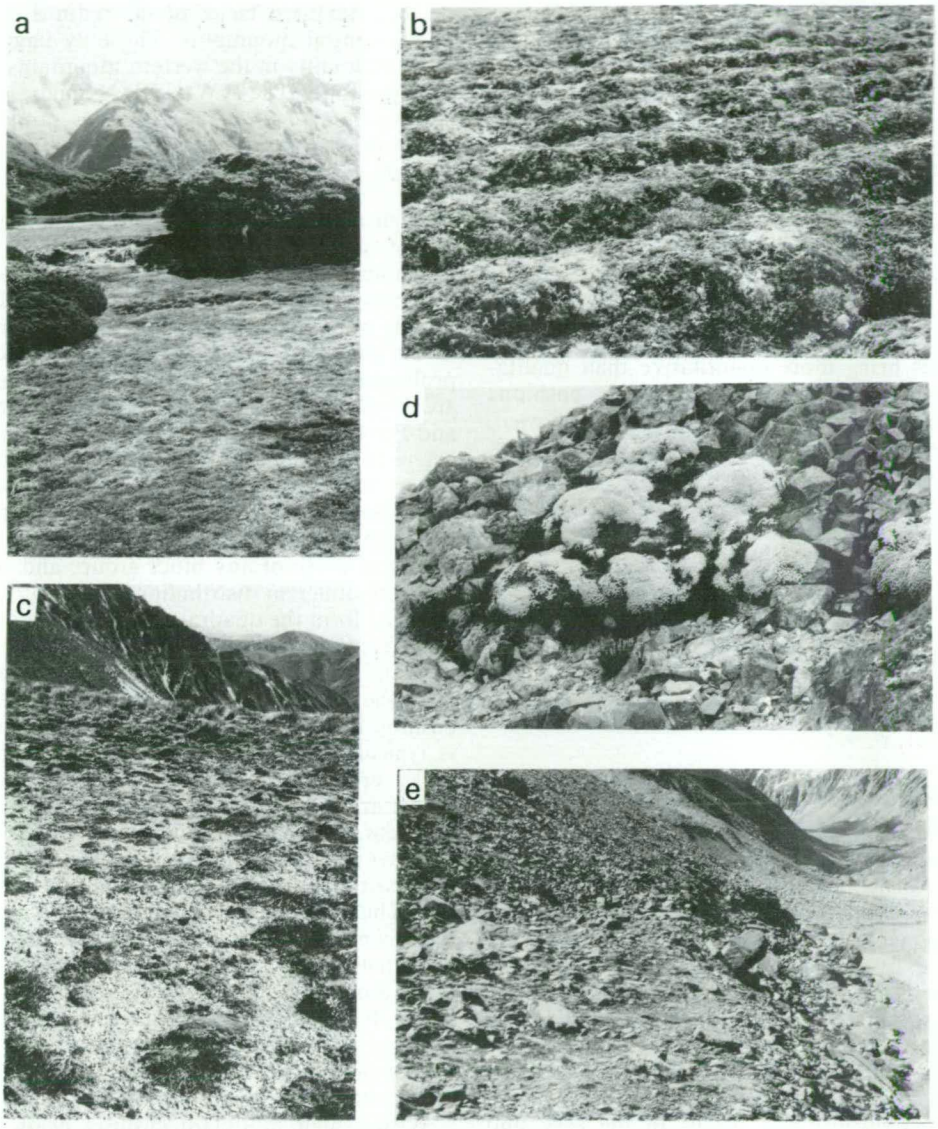

Fig. 5a *Donatia* cushion bog on Key Summit, Humboldt Mountains. **5b** High alpine cushion moor on Old Man Range, Central Otago showing inactive stripes common in this area. **5c** Alpine cushion herbfield on Mt. Peel, Canterbury. **5d** *Haastia pulvinaris* cushion rock community on Robert Ridge, Nelson Lakes. **5e** *Raoulia tenuicaulis* cushion shingle community above the Hooker glacier, Mt. Cook National Park.

Numerical analysis of Tasmania data

Bolster communities in Tasmania are generally referred to as bolster heaths or cushion heaths (Costin 1981, Kirkpatrick 1983). These names refer to the hard scleromorphic nature of most of the bolster species and the associated shrub element (e.g., *Epacris serpyllifolia, Sprengelia incarnata, Orites revoluta*, and *Orites acicularis*). Five types were recognised in Tasmania (Fig. 6, Table 2). Type 1 is a group of the east and central mountain quadrats dominated by the cushion species *Abrotanella forsteroides*. The quadrats in type 2 occur at high altitude, and are mostly dominated by *Phyllachne colensoi*. Types 3, 4, and 5 are centred on the western mountains and have high frequencies of *Donatia novae-zealandiae*, the differences between

Table 3 Percentage of species and genera shared between the six New Zealand cushion associations and the Tasmanian alpine flora.

Association	Species	Genera
Herbmoor	24.0	48.0
Cushion bog	20.5	37.2
High alpine cushion moor	8.2	38.8
Alpine cushion herbfield	8.4	31.8
Cushion rock	0.0	36.4
Cushion shingle	4.9	29.3

the groups being more quantitative than qualitative. Type 3 has a high frequency of the cushions *Dracophyllum minimum, Pterygopappus lawrencii,* and *A. forsteroides* in addition to *Donatia.* Types 4 and 5 have *Donatia* as the major cushion species. Type 5 is floristically similar to type 4, with lower frequencies of species group D and higher frequencies of species group A (Table 2).

The ordination shows two major groups (Fig. 6). The eastern/central group (type 1) forms one extreme and the western groups (types 2 to 5) the other extreme of the first axis. Axis 2 of the ordination was found to be significantly correlated to altitude of quadrats above climatic tree-line ($P < 0.0001$; $r^2 = 0.39$).

The Tasmanian associations and their environmental correlates

1. *Abrotanella forsteroides* cushion heath: (Fig. 7a) Quadrats of type 1 are predominantly composed of cushion heath dominated by *Abrotanella forsteroides,* and lack *Dracophyllum, Phyllachne,* and *Donatia.* The association is rare in the western mountains, occasional in the central mountains, and the sole cushion community in the eastern mountains (Fig. 8). In all cases *A. forsteroides* is strongly domed, with the interstices between the cushions dominated by either tussock grasses, hard graminoids, or scleromorphic shrubs in the east, and either hard graminoids or scleromorphic shrubs in the central mountains. The community is confined to those areas kept constantly moist through seepage, and thus is largely found in the valleys and low-lying parts of plateaus. Consequently, most of the quadrats in type 1 lie below the climatic tree-line, being not significantly different in this respect (χ^2, $P < 0.05$) from the quadrats in types 4 and 5. The quadrats in type 1 are highly significantly different in altitude ($P < 0.001$) from those in types 2 and 3. Species group G (Table 2) is characteristic of this community. The community is largely confined to dolerites and basalts. It appears to be absent from the quartzites and metamorphosed volcanics of the western mountains, and is present only on the finer-textured facies of the sedimentary rocks of the central mountains. The only large area of this community in the western mountains is found on limestone. The TWINSPAN analysis further divides type 1 into a relatively low rainfall group — 1A (higher score on axis 1 — Fig. 6 and 8) and a moderate rainfall group — 1B.

2. High mountain cushion heath: (Fig. 7b) Quadrats of type two are virtually restricted to the high mountain areas of central and western Tasmania, generally above 1250 m altitude (Fig. 8). They are usually well above the climatic tree-line, or if close to the climatic tree-line, in situations of relatively prolonged snow-lie. The characteristic dominants are *Phyllachne colensoi, Dracophyllum minimum,* and *Pterygopappus lawrencii* and the group is characterised by exclusively alpine species such as *Celmisia saxifraga* and *Phyllachne colensoi.* The quadrats in type 2 are significantly differently ($P < 0.05$) distributed in relation to the climatic tree-line than those of any other group, and have significantly different distribution in relation to parent material from the quadrats in all other groups with the exception of type 3.

At the generic level this community is very similar to the New Zealand *P. colensoi*-dominated alpine cushion herbfield (Table 1 and 2). In Tasmania, it is typically often sparse in cover with much bare rocky ground and with extremely shallow soils which are, however, at field capacity for much of the year, but can become relatively dry during summer drought (N. Gibson, unpublished data). The form of the cushion plants is only gently convex. The spaces between them are variously occupied by prostrate shrubs, rhizomatous rosette herbs and small tussock grasses, or by rocks, soil, or moss. High mountain cushion heath occurs on all rock types. It is probably precluded from the higher peaks of the eastern mountains because of the high degree of summer drought on sloping sites otherwise suitable for its occurrence (Fig. 8).

Within high mountain cushion heath *Pterygopappus* and *Phyllachne* tend to occupy more droughty sites than *Dracophyllum minimum. Dracophyllum* and *Phyllachne* tend to dominate around the edges of snow patches to the almost total exclusion of *Pterygopappus* (Gibson & Kirkpatrick 1985).

3. Mosaic cushion heath: (Fig. 7c) Most of the quadrats in type 3 fall within this physiognomic grouping, which is characterised by an almost total cover of cushion plants of many species. The complex species mixtures create a mosaic of many different colours and textures on the gently undulating surface of the cushion heath. The cushion plants widely present are *Donatia novae-zelandiae, Carpha rodwayi* W. M. Curtis, *Mitrasacme archeri,*

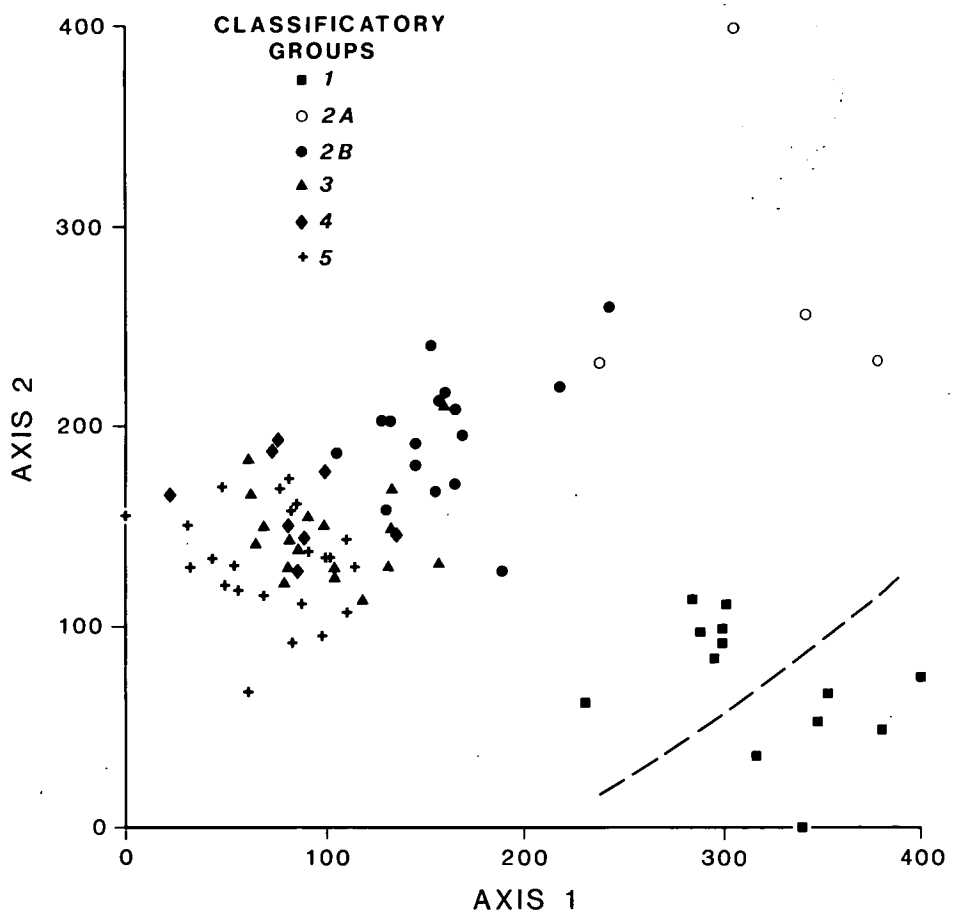

Fig. 6 Ordination of Tasmanian data set showing classificatory groups. Group 1 is further subdivided by the dashed line into group 1A, a relatively low rainfall group (high score on axis 1) and group 1B, a moderate rainfall group.

Dracophyllum minimum, Oreobolus pumilio, and *Abrotanella forsteroides*. Examples of this community have been described by Gibbs (1920), Sutton (1928), Kirkpatrick (1980), Kirkpatrick & Harwood (1980), and Kirkpatrick & Gibson (1984).

On any one mountain, mosaic cushion heath will tend to occur at higher altitudes than both *A. forsteroides* cushion heath and *Donatia* cushion heath, and at lower elevation than the high mountain cushion heath, these differences being reflected in the significantly different ($P < 0.05$) distribution in relation to the climatic tree-line of the quadrats in type 3 when compared to those in each of the other groups. However, related edaphic factors may account for more of this pattern of variation than does any gradient in temperature conditions. Mosaic cushion heath occupies more constantly moist sites than those occupied by the often adjacent high mountain cushion heath.

4. *Donatia novae-zelandiae* cushion heath: (Fig. 7d) This community largely corresponds with types 4 and 5 of the TWINSPAN classification, with species group A being characteristic. *Dracophyllum minimum, Phyllachne*, and *Abrotanella forsteroides* are absent from most of the quadrats referable to this community. The *Donatia* cushions are domed, but slightly less so than those of *A. forsteroides*. The interstices between the *Donatia* cushions are characteristically occupied by hard graminoids and scleromorphic shrubs. *Isophysis tasmanica* is the most prominent of the former, and *Microcachrys tetragona* (a gymnosperm) and *Epacris serpyllifolia* are the most notable of the latter.

Types 4 and 5 are predominantly, but not totally, subalpine, and both are concentrated on the poorest of the alpine soils, largely those formed on quartzitic rocks, in the high rainfall region of the west of the state (Kirkpatrick & Dickinson 1984,

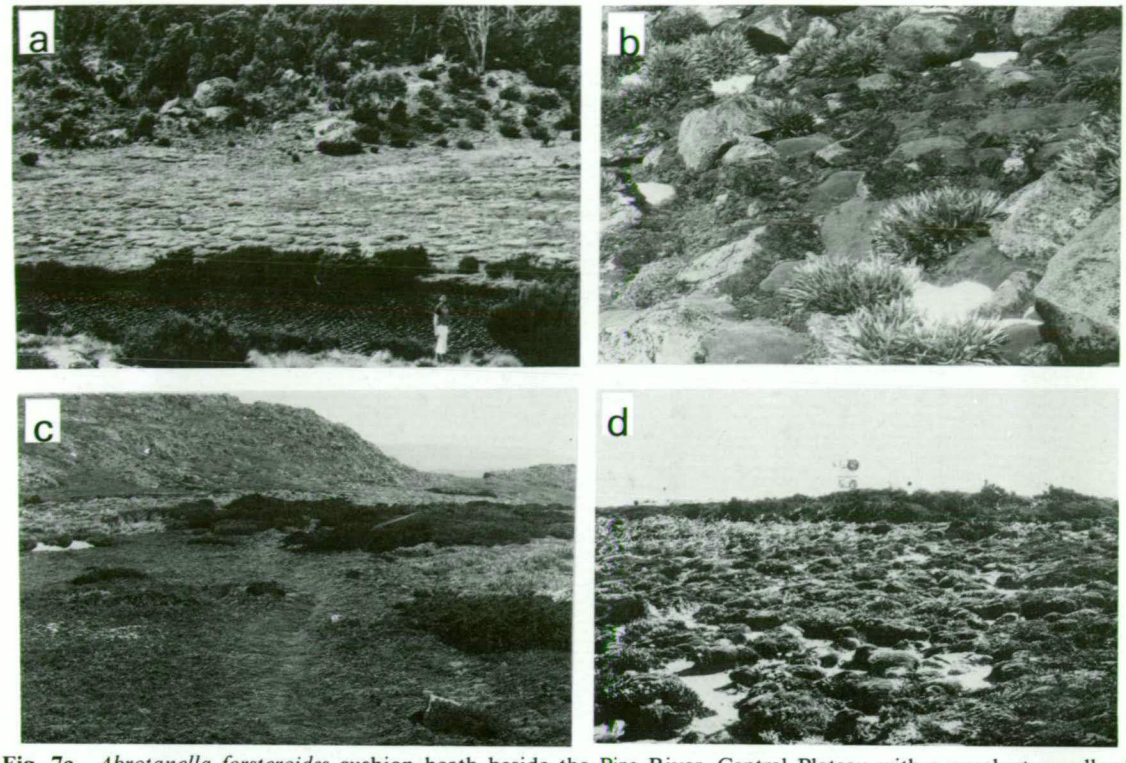

Fig. 7a *Abrotanella forsteroides* cushion heath beside the Pine River, Central Plateau with a eucalypt woodland occurring on the higher ground. **7b** High mountain cushion heath dominated by *Phyllachne colensoi* and *Astelia alpina* in a snow patch on the Snowy Range. **7c** Mosaic cushion heath on Mt. Field West. **7d** *Donatia* cushion heath which was burnt 17 years ago on Mt. Read.

Kirkpatrick 1984) (Fig. 8). Types 4 and 5 differ significantly from each other ($P < 0.05$) only in aspect, with type 4 occurring mainly on southerly aspects and type 5 occurring mainly on northerly aspects. Like type 3, types 4 and 5 are absent from the eastern mountains.

Comparison of the New Zealand and Tasmanian patterns

The New Zealand cushion associations are very distinct from each other, much more so than those found in Tasmania (Table 1 and 2). This phenomenon is not considered to be an artifact of the differing sampling frequencies. The two most likely reasons accounting for this difference are considered to be the much more subdued relief of Tasmania and its lack of extensive alpine and subalpine grasslands compared to New Zealand.

Tasmania, due to its more subdued relief, lacks two of the locally distinct habitats in which cushion plants dominate in New Zealand, river shingle and high alpine shattered rock fields. The percentage of species the groups typical of these habitats share with the Tasmanian alpine flora is very low (Table 3).

Tasmania also completely lacks an equivalent to the New Zealand high alpine zone (Wardle 1964); if the climatic tree-line were to rise as little as 300 m, the alpine zone proper would be eliminated. Tasmania has therefore no equivalent to the central Otago high alpine cushion moor (Table 3). The lack of the high alpine habitat also largely accounts for the major differences in the distribution pattern of *Phyllachne colensoi* between these two areas (Fig. 9). This species is widespread in New Zealand from the upper low alpine zone on areas of shallow soils, into the high alpine. In Tasmania it is recorded from only 12 locations and is generally restricted to areas above 1250 m on well drained sites or rocky slopes, often associated with snow patches.

In New Zealand *Donatia* is restricted to bogs due to competition from snow tussock grasses (Burrows 1977, Dobson 1979), whereas in the western Tasmanian mountains extensive *Donatia* cushion heaths (herbmoors) occur over a wide range of soil

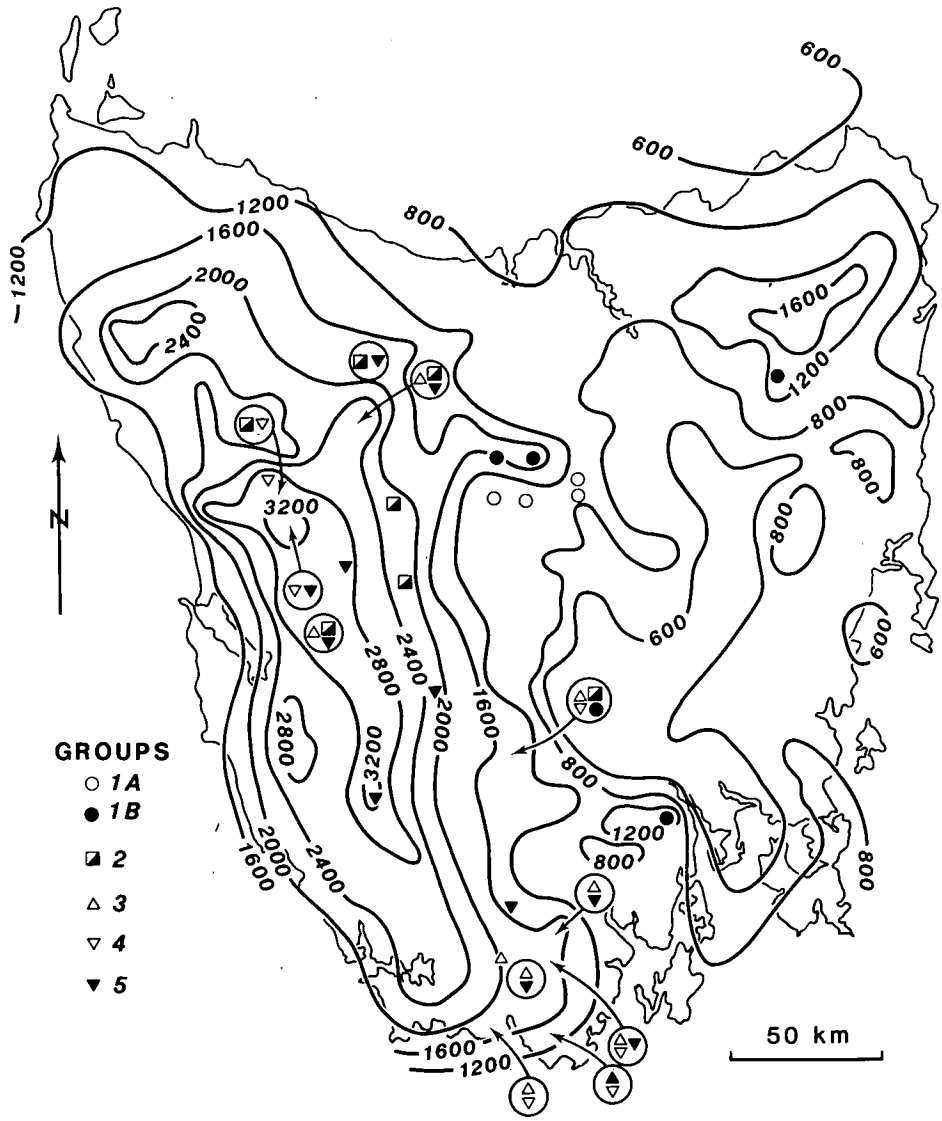

Fig. 8 The distribution of the classificatory groups in Tasmania in relation to precipitation (mm). Some symbols represent more than one quadrat. (Rainfall data from Bureau of Meteorology — unpublished data.)

moisture conditions. Western and central Tasmania have few subalpine or alpine grasslands, the alpine vegetation being largely dominated by shrub species (Kirkpatrick 1982, 1983). Alpine grassland development has generally been correlated with long and persistent snow-lie (Billings & Mooney 1968), although it may also be related to edaphic factors (Kirkpatrick 1982). Snow-lie of any duration, except in localised snow patches, is the exception in Tasmania, due to its relatively low relief and maritime climate (Fig. 2).

The distributional patterns of *Donatia* in both countries is, none the less, remarkably similar (Fig. 9), with the species being concentrated in the high rainfall regions of the west and south under the influence of the westerly wind systems and mountain barriers. *Donatia* extends down to sea-level on the Awarua Plain near Invercargill in New Zealand and to 80 m a.s.l. in the Hardwood Valley in western Tasmania (M. Brown pers. comm.) in habitats where competition from lowland species is decreased by acid soils and high water tables.

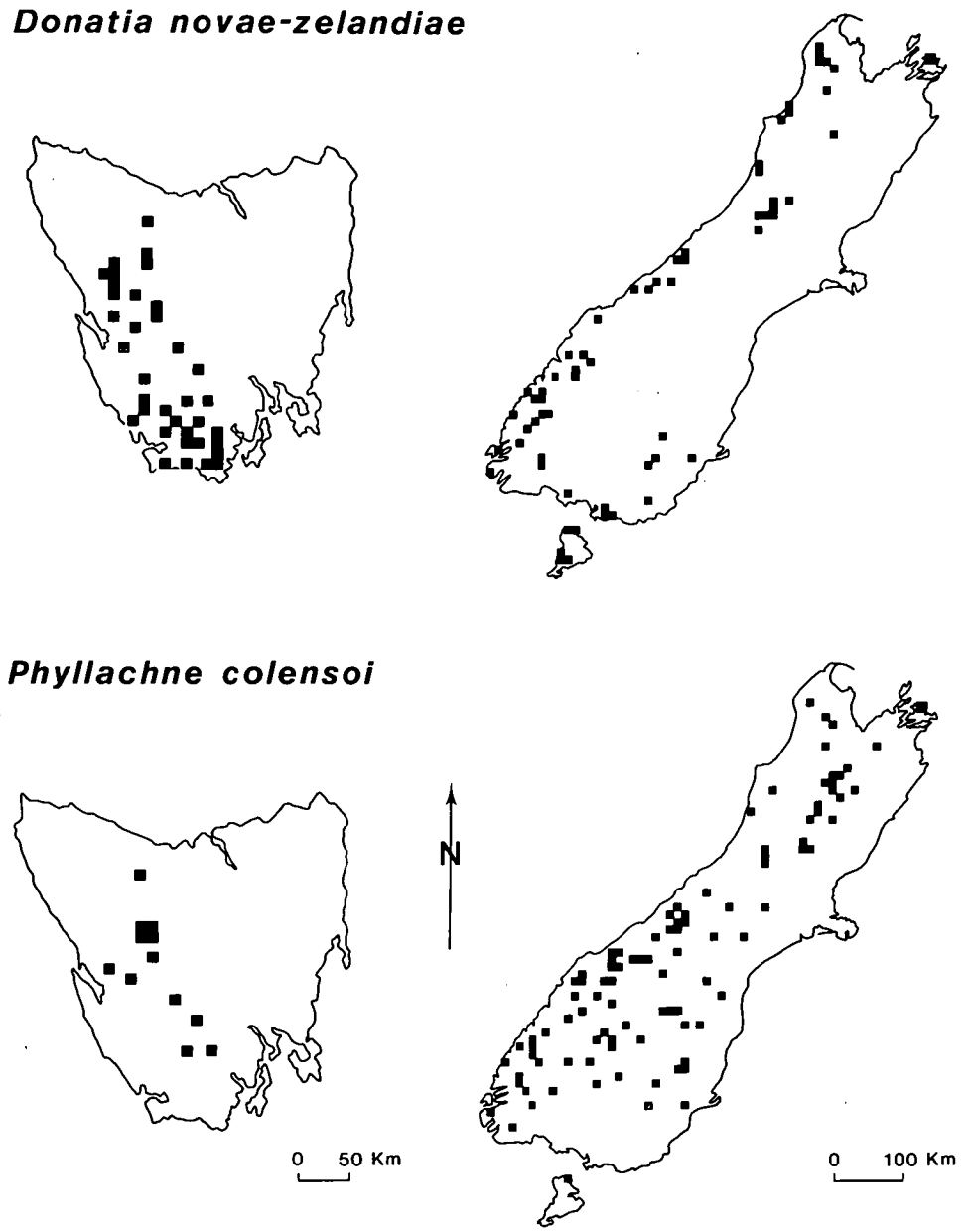

Fig. 9 Distribution patterns of *Phyllachne colensoi* and *Donatia novae-zelandiae* in both Tasmania and New Zealand, on a 10 km square grid.

ACKNOWLEDGMENTS

We would like to thank Prof. A. F. Mark, Prof. G. T. S. Baylis, Dr D. Given, Ms B. Macmillian, Mr M. Heads, and Ms A. Turner for assistance to one of us (N. G.) during a summer field trip to New Zealand, and the journal referees for their constructive comments.

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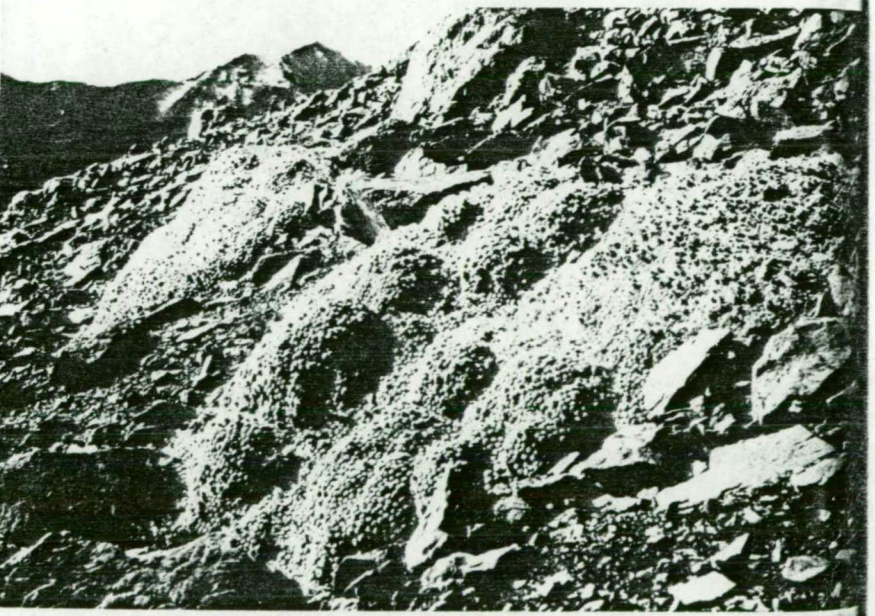

Haastia pulvinaris (vegetable sheep), a characteristic growth form on screes and similar habitats, on Mt Fyffe, New Zealand. Photo D.R. Given

CHAPTER FIVE

ON THE ORIGIN AND EVOLUTION OF AUSTRALASIAN ALPINE CUSHION PLANTS

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INTRODUCTION

Cushion plants are an unusual lifeform common in the alpine and subalpine regions of Australasia. They are closely compacted cryptophytes or hemicryptophytes and are best developed in the mountain areas of southern New Zealand, Tasmania and the subantarctic Macquarie Island. The cushion form may be produced by several different structural morphologies, and a precise definition of the term cushion plant is difficult. As well, some species are facultative cushions, producing the cushion form in only some environments. In his worldwide survey of cushion plants, Rauh (1939) used the term for any species that was capable of producing a recognizable cushion. He subdivided cushion plants into 5 primary types on gross structural morphology (Table 1), though not all categories are mutually exclusive even in the adult stage. His system is followed here. The hard bolster species common in the Tasmanian and New Zealand mountains fall into his spherical and compact cushions (types 1c, 1d and 3 - Table 1).

The cushion lifeform has been recorded from at least 34 different families worldwide (Godley 1978). This figure includes cushions from lowland as well as alpine habitats. Besides the Australasian alpine regions, cushion plants are also very common in South America (Pisano 1983), the subantarctic islands (Huntley 1972) and the tropical paramo regions (Hope 1976). This lifeform appears less common in the alpine regions of the northern hemisphere. In this paper we have confined our discussion to the Australasian region encompassing Tasmania, southern New Zealand, New Guinea and Macquarie Island. Certain lower altitude communities are not included, such as the Sphagnum bogs, and lower plants are not analyzed except for one species on Macquarie Island. The origin and evolution of this lifeform are discussed.

Plant nomenclature follows Curtis (1963; 1967) and Curtis and Morris (1975) for Tasmania; Allan (1961), Moore and Edgar (1970), Healy and Edgar (1980) and Mark and Adams (1979) for New Zealand; Royen (1980) for New Guinea; and Taylor (1955) for Macquarie Island.

Table 1. Rauh's classification of cushion plant types, where cushion plant is defined as any species capable of assuming a cushion form (Rauh 1939). Symbols in brackets are abbreviations used in the text

1. TRUE CUSHION PLANTS
The cushion form in these species is genetically fixed and results from the systematical relationship of the even radial growth of numerous often closely packed meristems with little apical dominance, resulting in flat hemispherical surfaces. In compact species peat accumulation results. These species have a persistent tap root, though adventitious roots may also develop.

a) Tree cushions (TC)

b) Spherical shrubs (ShC)

c) Spherical cushions proper: non peat-accumulating (SC)
: peat-accumulating (SCp)

d) Flat cushions: non peat-accumulating (FC)
: peat-accumulating (FCp)

2. CREEPING CUSHIONS (CC)
Those species of mat cushion which form by lateral branches spreading in all directions and which root adventitiously from nodes. Persistent taproot present.

3. COMPACT CUSHIONS (CoC)
Morphologically identical to true cushion plants. However a persistent taproot is replaced by adventitious rootlets.

4. ROSETTE CUSHIONS (RC)
Formed by the production from a young plant of lateral branches with a terminal rosette which in turn roots and produces further rosettes, generally with gradually decreasing internode length. The result is a dense solid cushion of somewhat interconnected rosettes.

5. CUSHION MOSSES (CM)
All moss species that produce the cushion form.

TASMANIA

In Tasmania there are 4 main cushion communities which can intergrade with each other (Gibson and Kirkpatrick 1985). These are:

1) Abrotanella forsteroides cushion heath This community occurs widely on the dolerite and basalt mountains of eastern and central Tasmania. It occurs both above and below the treeline, and is most prevalent in areas of poor drainage. Thus it is found largely in valleys and low lying parts of plateaus. Abrotanella may form individual cushions of up to 80 cm in diameter and 30 cm high, and coalesce into extensive mats. This species, like all Tasmanian bolsters except for Dracophyllum minimum, lacks a persistent taproot and is a compact cushion under Rauh's classification (Table 1).

2) High mountain cushion heath: This community is restricted to Tasmania's highest mountains (above 1250 m), and is dominated by the bolster species Phyllachne colensoi, Dracophyllum minimum and Pterygopappus lawrencii. This community is generally found well above the climatic treeline. Phyllachne colensoi is one of Tasmania's few obligate alpine species, being recorded from only 12 high altitude locations state wide. This community is found in the driest of the cushion plant habitats, including the skeletal soils of quartzite snowpatches and the edges of boulder fields (Fig. 1).

3) Mosaic cushion heath: This community is found on the plateau tops

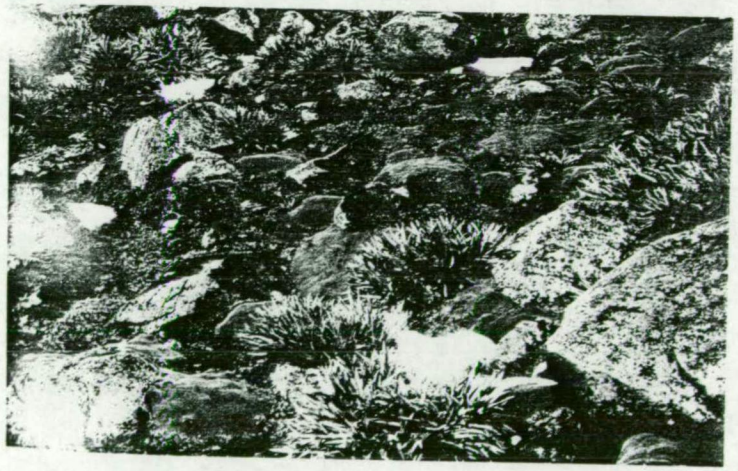

Fig. 1. High mountain cushion heath, Snowy Range, Tasmania (1300 m). Phyllachne colensoi dominated community occupying a snow patch; Astelia alpina is the large graminoid and Pentachondra pumila is the dark mat creeping over dolerite boulders. Photo: N. Gibson

of the central Tasmanian dolerite mountains. It is formed by the coalescing into extensive mats of many cushion species, including Donatia novae-zelandiae, Dracophyllum minimum, Abrotanella forsteroides, Carpha rodwayii, Mitrasacme archeri and Oreobolus pumilio, resulting in a beautiful gently undulating surface of many different colours and textures, which may cover large areas.

4) Donatia novae-zelandiae bolster heath: This community is found in the high rainfall regions of the western quartzite mountains on poor soils, and is totally absent from the eastern mountains. This species occurs over extensive areas in Tasmania and is not restricted to bog situations as in New Zealand. A closely related species, Donatia fascicularis, does occur in bog situations in South America.

The floristic east-west gradient shown by the cushion plant communities has also been reported for the Tasmanian alpine flora in general (Kirkpatrick 1982).

Soil moisture is only rarely limiting in most of these communities. Individual cushion species show some preference for the extremes. Phyllachne colensoi and Dracophyllum minimum can occupy better drained sites, while Carpha rodwayii is most common on the most waterlogged sites of the mosaic bolster heath. In addition to the cushion species already mentioned several other cushion species occur in these and other alpine communities (see Appendix).

There is an interesting occurrence of the New Zealand bolster species Chionohebe aff. ciliolata var. fiordensis on the dolerite bluffs of Ben Lomond in the northeast of the state.

NEW ZEALAND

On the South Island of New Zealand, there are 6 very distinct alpine cushion communities (Gibson and Kirkpatrick 1985). These have been described as:

1) Stewart Island cushion herbmoor: Physiognomically most similar to the Tasmanian bolster heaths, it is dominated by the bolster species Donatia novae-zelandiae and Raoulia goyenii. This community occurs on relatively flat areas of high soil moisture above about 600 m on Mt Anglem. It is apparently more widespread on the mountains south of Pattersons Inlet (H.D. Wilson pers. comm.). Elsewhere in New Zealand, unlike Tasmania, Donatia is restricted to bog situations. Burrows (1977) and Dobson (1979) suggested that this restriction is due to competition from snow tussock grasslands (Chionochloe spp.) though it may also be related to edaphic factors.

2) Donatia novae-zelandiae cushion bogs: The cushion bogs are common in the high rainfall areas of the west and south under the influence of the westerly wind systems. They tend to occur as small areas with poor drainage, and are often surrounded by snow tussock grassland. Dobson (1979) suggested that this community forms on oligotrophic sites where the mean annual temperature is less than 6°C.

3) Alpine cushion herbfield: This subassociation within the snow tussock grasslands becomes more dominant with increasing altitude. It is usually dominated by Phyllachne colensoi or Celmisia sessiliflora, and occasionally, on fresh high alpine moraines, by Colobanthus spp. The community appears on skeletal soils in the low alpine grasslands and extends into and becomes dominant on the more protected sites of the high alpine zone. This is the most widely distributed of the New Zealand cushion communities and is found throughout the mountain areas of the South Island.

4) High alpine cushion moor: This community is confined to the schistose mountains of the Central Otago region. It is dominated throughout by the trailing non-peat forming cushion Dracophyllum muscoides (Fig. 2). This community occurs over large areas of these mountains from wind exposed fjaeldmark where surface cover may be less than 20 percent, to more sheltered locations where cover may be complete (Mark and Bliss 1970). On the most exposed sites the Dracophyllum cushions are gradually migrating across the landscape, eroding on their windward edge and actively expanding on their lee edge (Mark and Bliss 1970).

Fig. 2. High alpine cushion moor, Old Man Range, New Zealand (1800 m). Dracophyllum muscoides dominated community, common in the high alpine zone of Central Otago; several other cushion species also occur including Phyllachne colensoi and P. rubra. Photo: N. Gibson

5) Cushion rock communities: The cushion communities that occupy the high alpine shattered rock areas of the northern Canterbury Alps make up the fifth cushion community of the South Island. These are generally dominated by the large yellow Haastia pulvinaris bolster. This and similar cushion species are first to invade the shattered rock and associated colluvial areas and provide protected sites in which other species may establish. A community similar in species composition to the alpine cushion herbfield may eventually develop.

6) River shingle cushion communities: These cushion communities form on the unconsolidated river shingles of the braided river valleys of

subalpine and alpine New Zealand. The shingle is initially dominated by the creeping cushions Raoulia tenuicaulis, R. australis and R. glabra. These species stabilize the shingle and allow humus accumulation. This community, like the rock community, is seral and is in turn invaded by herbs and graminoids which results eventually in a closed tussock grassland.

AUSTRALIA

The cushion form is poorly developed in the Australian Alps. It is a common life form in only 2 of the alpine communities (Costin et al. 1979). In the Epacris-Chionohebe wind fjaeldmark, the cushion species Colobanthus pulvinatus is found as small cushions between the broken rock and gravel. This community occurs as a narrow band on the most exposed ridge tops which are periodically subjected to high winds.

Another Colobanthus species, C. nivicola, occurs as the codominant in the Coprosma-Colobanthus snowpatch fjaeldmark under semipermanent snowpatches. In neither situation do the cushions grow to more than 10 cm diameter, and in both communities total plant cover is low. Several other cushion species occur in these and other alpine communities in the Australian Alps (see Appendix). Of interest is the creeping cushion Pentrachondra pumila, a species which also occurs widely in Tasmania where it rarely has a distinct cushion habit.

MACQUARIE ISLAND

There are 3 cushion dominated communities in the depauperate vegetation of subantarctic Macquarie Island. One of these is dominated by a very distinct moss cushion.

1) Azorella selago fjaeldmark: This community occurs on the more exposed areas of uplifted plateau above 300 m. Like the high alpine cushion moor (Central Otago, New Zealand), this community is subject to extremely high winds. On Macquarie Island high winds are fairly constant, averaging more than 20 knots at sea level (Taylor 1955). In the most exposed areas of the plateau, cover falls below 10% and the cushions appear to be migrating across the landscape in front of the wind (Ashton and Gill 1965).

2) Colobanthus muscoides tor and bog communities: This species forms the dominant vegetation on both the coastal rock tors occurring along the coast, and in the bogs of the west coast terraces. Colobanthus muscoides appears to be highly resistant to both salt spray and wind dessication, forming dense cushions or mats up to 60 cm diameter and 20 cm deep on the coastal rock tors. In the bogs on the west coast it adopts a mat form (Taylor 1955).

3) Ditrichum strictum fjaeldmark: The moss Ditrichum forms another type of cushion fjaeldmark on the exposed plateau of Macquarie Island. It generally forms small cushions up to 30 cm in diameter on very exposed sites (Ashton and Gill 1965).

NEW GUINEA

Four communities in which cushion taxa are important have been described from New Guinea (Hope 1976; 1980). Many of the taxa involved are endemic to single mountain areas, so that the detailed community floristics vary considerably.

1) Hard cushion bog: This is a subalpine bog forming on waterlogged acid peats from 2850 m to 4200 m altitude. The dominant widespread cushions are Oreobolus pumilio, Centrolepis philippinensis, Plantago polita, Astelia alpina and Danthonia oreoboloides, forming hard, slightly domed flat mats with tufts of herbs growing between the cushions. Other characteristic species have restricted distributions. From Mt Giluwe westward the remarkable cushion shrub Rhododendron saxifragoides forms cushions up to 50 cm high and 2 m in extent, though usually much smaller. Asanthomyrtus and Vaccinium form loose flat mats on its margins. Shrubs are absent in the eastern mountains and the flora is generally much simpler, although interesting cushion endemics such as Sagina donatoides and various Eriocaulon and Poa species occur there.

The bogs are not extensive, and form a mosaic with grass bogs or sedge fens, in both of which many cushion species also occur. Grass invasion seems to reflect better nutrition and less waterlogging. In the east, volcanic ash falls enhance nutrition and slightly more seasonal climates also occur. These factors may explain the poorer flora and restricted distribution of the hard cushion bog, east of Mt Giluwe.

2) Astelia alpina bog: This bog consists of masses of hard hummocks of silvery Astelia up to 30 cm high and 50 cm across, often in pure stands in alpine areas above 3800 m (Fig. 3). Centrolepis, Plantago and moss cushion taxa, and the fern Gleichenia vulcanica may also occur. The community is common on gentle seepage slopes. Astelia alpina also occurs in the Australian Alps and Tasmania, where it generally forms extensive mats on seepage lines.

3) Carpha alpina fen: Carpha alpina forms isolated small cushions which sometimes enlarge and form rings on bare peat or mineral substrates subject to regular inundation (Fig. 4). In Irian Jaya the local endemic variety of Potentilla foersteriana var. brassii and Eriocaulon montanum contribute mats of hard rosettes, and mosses are common. Carpha alpina also occurs in moss tundras above 4400 m, again usually on mineral soils, sometimes with a tuft habit. This species also occurs widely in New Zealand, Australia and Tasmania, where it is only observed rarely as a cushion.

4) Sagina belanophylla open herbland: This community was described (as Scleranthus singuliflorus open herbland) by Hope (1976) from Mt Jaya, occupying areas of recent glacial retreat above 4200 m. There is a very open scattering of small cushions, together with tufts or mats of Epilobium detznerianum and Parahebe wollastonii. Various mosses such as Racomitrium form mats in older areas. This community is clearly successional, pioneering the establishment of vegetation on bare till subject to nightly frosts and needle ice on almost all days of the year.

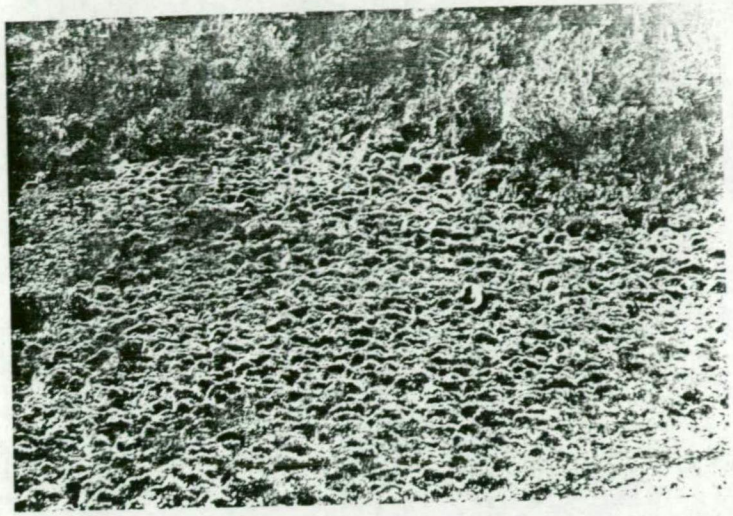

Fig. 3. Astelia alpina bog, Star Mountains, New Guinea (3550 m). A bog showing numerous hummocks of A. alpina, well below treeline. Photo: G. Hope

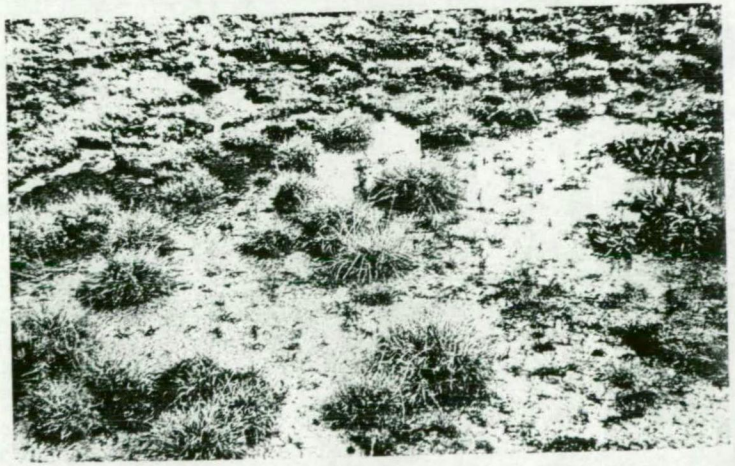

Fig. 4. Carpha alpina fen, Mt Jaya, New Guinea (4250 m). A fen dominated by small cushions of the sedge C. alpina. Photo: G. Hope

There is a close parallel with the New Zealand river shingle Raoulia communities.

Although this community is restricted at present, its component species are widespread, though uncommon, on non-glaciated mountains elsewhere in New Guinea. It is likely that in the Pleistocene this community was important near the fluctuating ice sheets.

ORIGINS OF THE CUSHION FORM

The cushion lifeform occurs in 27 families of higher plants (Appendix) and in many different environments of the Australasian alpine zone, from bogs to shattered rock and from snowpatch to herbfield. It would appear therefore that there is no single causal factor responsible for the origin of the cushion form. Furthermore, in any one environment it is generally impossible to suggest any single selective pressure as being responsible for selection of this lifeform.

In New Zealand, New Guinea and Macquarie Island the cushion dominated communities are generally quite specific to particular geomorphic environments, unlike Tasmania where interacting edaphic factors appear to control cushion community distribution.

The communities may be broadly classed as either swamp or fjaeldmark types, again with Tasmania as the exception. The former are more typical of the tropics and very cool moist environments in which energy and nutrients are probably limiting. The cushion form can colonize water-logged peats, and helps to maintain high water tables which prevent the invasion of dryland species.

In fjaeldmark situations, the cushion form successfully colonizes cold and disturbed environments. Wind and frost heave play a major role in the destabilizing of alpine surfaces, with wind effects increasing with increasing latitude. Again energy limits presumably play a role in preventing competition. Environments with high wind can profoundly effect the nature of the vegetation found there. Two such environments can be discerned on Macquarie Island and in Central Otago, New Zealand.

In Central Otago, the extreme severity of the northwesterly storms that lash these mountains can be seen from the pattern of lichen encrustation on the schist tors. The northwesterly faces are completely clean to a height of 3 m or more, while on the protected sides a profusion of encrusting lichens extends right to ground level. Macquarie Island at 54°S is situated within the roaring fifties. Average wind speeds on the plateau are at least 25 knots and probably much higher (Taylor 1955). Wind gusts in excess of 100 knots have been recorded at sea level.

In both cases the extremely flat, ground hugging nature of the vegetation, including the cushion forms, is likely to be primarily a result of the wind. Any tall vegetation would very quickly suffer extreme dessication and abrasion in these environments. In this type of environment the cushion form often dominates.

In Tasmania the classification into swamp or fjaeldmark types breaks down somewhat. The Abrotanella cushion heath does occur in areas of poor drainage and high water table. However, the other cushion communities are generally quite dry to walk on, due to the hard nature of the bolsters,

even when the water table is close to the surface. The high mountain cushion heath, like the New Zealand high alpine cushion moor, may form a fjaeldmark, but can also become dominant in closed communities.

In most alpine environments it is not possible to identify any single limiting environmental factor as being responsible for the cushion form. In most cases examined it appears that the cushion habit is genetically fixed (Poweraker 1917; Gibson, unpub.). Though many cushion species appear capable of growing at lower altitude, their slower growth rates preclude them from doing so except on those sites where the normal lowland vegetation is excluded. Examples of such exclusions are found on the highly acid peats of the Hardwood Valley, Tasmania (83 m elevation) and the Awarua Plains (sea level) of the South Island, New Zealand, where the bolster species Donatia novae-zelandiae and other associated alpine species are found (Crosby-Smith 1927; M. Brown, pers. comm.).

The alpine environment in which this life form occurs is extremely rigorous. The stresses imposed on plant growth may include low temperature, short growing season, periods of snowlie, severe frost action, high wind, ice ablation, physical drought and physiological drought. As a consequence of these stresses primary production is generally low. Mooney and Dunn (1970) theorized that similar life forms may develop independently in similarily stressed geographically isolated habitats. This results because as the stresses imposed by an environment are compounded, the number of biological solutions becomes increasingly limited. The cushion lifeform appears to support this theory, given the number of compounded stresses imposed by the alpine environment and the widespread occurrence of cushion plants in these environments. This lifeform has evolved from a large number of different families and from a number of different floras. It is likely that it has evolved a number of times. The mountains of New Guinea and New Zealand are considered to be young (Raven 1973; Fleming 1963), while the mountain areas of Tasmania and Australia are thought to be of considerable antiquity (Jones and Veevers 1982; Ollier, this volume). The high degree of endemism of cushion species suggests that local and independent evolution of this lifeform has been common (see Appendix).

Not all cushion taxa show restricted distributions. Azorella selago has a circumantarctic distribution. The most likely explanation for this distribution pattern is long distance dispersal by wind or birds. In New Guinea, a few northern taxa have contributed to the cushion flora, such as Rhododendron and Potentilla. The shared Tasmanian and New Zealand species of Donatia and Phyllachne and the occurrence of these genera in South America may, on the other hand, indicate a Gondwanic origin of these genera.

Centrolepis philippinensis and some other taxa occur both in New Guinea and Borneo. Other species that are even more widespread at present (e.g. Gaimardia setacea, Astelia alpina and Scleranthus singuliflorus) are likely to have distributions resulting from long distance dispersal, rather than vicariance, as Smith (1977) has argued, although the relative importance of the first two species in New Guinea habitats argues against recent arrival (Appendix).

The appearance of many species in the one genus, for example Raoulia in New Zealand or Eriocaulon in New Guinea, usually reflects allopatric speciation, presumably triggered by fluctuating connections between ranges due to climatic change. In New Guinea both bog and fjaeldmark habitats

are relatively restricted during the present interglacial, and would have been favoured by the harsher and more fluctuating conditions of the glacial maximum (Hope, this volume). Glacial times would similarly have expanded fjaeldmark biozones in other areas. Active speciation is also indicated by the existence of cushion and non-cushion habits in the same species. Poa papuana is a widespread tuft species, but only in the Owen Stanley Range does subsp. pulviniformis form small dense cushions. Drapetes ericoides, not a cushion species, adopts a dense mat form on Mt Jaya, but elsewhere is a straggling low bush. In Tasmania, a common shrub of the lowland button grass plains Sprengelia incarnata is reduced to a very small dense mat less than 1 cm in height, which occasionally takes on a cushion shape in alpine areas. As noted above several species have gained a cushion habit, representing a probable genetic shift, in part of their range, e.g. Carpha alpina, Astelia alpina and Pentachondra pumila.

Table 2. Vascular cushion plant taxa in common between areas, by number (lower left) and percentage (upper right). New Zealand data from South Island only; Australian data from Australian Alps

FAMILIES

	New Guinea	Australia	Tasmania	New Zealand	Macquarie I
New Guinea	16	41%	36%	43%	22%
Australia	5	8	70%	60%	20%
Tasmania	5	7	12	75%	14%
New Zealand	6	6	9	12	29%
Macquarie I	2	1	1	2	2

GENERA

	New Guinea	Australia	Tasmania	New Zealand	Macquarie I
New Guinea	25	32%	41%	33%	0%
Australia	4	10	60%	36%	17%
Tasmania	7	9	20	58%	9%
New Zealand	6	5	11	18	10%
Macquarie I	0	1	1	1	2

SPECIES

	New Guinea	Australia	Tasmania	New Zealand	Macquarie I
New Guinea	47	4%	11%	6%	0%
Australia	1	11	37%	10%	0%
Tasmania	4	7	27	18%	0%
New Zealand	3	3	7	49	0%
Macquarie I	0	0	0	0	2

Percentages calculated by: 200C/A+B, where A = no. of taxa in area 1; B = no. of taxa in area 2; C = no. of taxa common between areas 1 & 2

Table 2 shows that while there are some strong relationships between the floras at family and generic level, each area has produced its own species suite, although Tasmania and Kosciusko share sufficient species to support the idea of some species exchange between the areas. The New Zealand-Tasmanian communality may suggest the same exchange at generic level.

Despite the low correlation between cushion plant taxa in New Guinea and those of other areas, many of the families and genera, from which cushion plants are derived, are shared. The presence of cushion grasses and Eriocaulon in New Guinea, in families without cushion representatives elsewhere, can be contrasted with the absence of cushions of Scrophulariaceae or Epacridaceae there. Genera such as Drapetes, Parahebe and Trochocarpa grow in cushion communities but have not yet produced cushion species in New Guinea, although the families (Thymeleaceae, Scrophulariaceae, Epacridaceae) have cushion species in Tasmania and New Zealand. This suggests that many cushion taxa have evolved independently.

Because of their slow growth, cushion communities are particularly sensitive to trampling by cattle or walkers (Gibson 1984), although they are adapted to colonizing bare ground and can be useful pioneer species in revegetating disturbed ground, albeit slowly. Their fluctuating habitats at successional and longer timescales provide an explanation for the evidence that most species are still actively evolving.

The cushion lifeform thus appears to be particularly well adapted to the tropical and maritime alpine as well as the subantarctic environments. There is evidence for both a long history of this lifeform (e.g. Donatia and Phyllachne) as well as continuing active speciation. Detailed ecological and physiological studies will be needed to fully understand the success of this lifeform in these environments.

SUMMARY

Species distribution patterns indicate that the cushion habit has evolved at several different times in several different regions. Only rarely does a single limiting environmental factor appear to be associated with the occurrence of this lifeform. It appears that the cushion habit is one of a limited number of biological solutions available in an environment with a large number of compounded stresses. Local evolution of the cushion form appears to have occurred in most alpine environments. The evolutionary history of cushion taxa with wider distribution patterns is open to several interpretations, although it is likely to include long distance dispersal and continuing allopatric speciation.

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APPENDIX

Species of Australasian cushion plants by family, including endemic status (+ = endemic; ++ = very restricted endemic) and cushion type (abbreviations as for Table 1)

FAMILY/SPECIES	ENDEMIC STATUS	CUSHION TYPE
TASMANIA		
CARYOPHYLLACEAE		
Scleranthus biflorus	-	FCp
S. uniflorus	-	FCp
CENTROLEPIDACEAE		
Centrolepis monogyna	+	CoC
C. muscoides	+	CoC
Gaimardia fitzgeraldii	+	CoC
G. setacea	-	CoC
COMPOSITAE		
Abrotanella forsteroides	+	CoC
Ewartia meridithae	+	CC
Helichrysum milliganii	+	RC?
Pterygopappus lawrencii	+	CoC
CYPERACEAE		
Carpha alpina[1]	-	CoC
C. rodwayii	+	CoC
Oreobolus acutifolius	+	CoC
O. oxycarpus	-	CoC
O. oligocephalus	+	CoC
O. pumilio	-	CoC
DONATIACEAE		
Donatia novae-zelandiae	-	CoC
EPACRIDACEAE		
Dracophyllum minimum	+	ScP
Pentachondra pumila[2]	-	CC
Sprengelia incarnata	-	FC?
LILIACEAE		
Astelia alpina[3]	-	CoC
LOGANIACEAE		
Mitrasacme archeri	+	CoC
SCROPHULARIACEAE		
Chionohebe aff. ciliolata var. fiordensis	-	ScP
STACKHOUSIACEAE		
Stackhousia pulvinaris	-	CC
STYLIDIACEAE		
Phyllachne colensoi	-	CoC
THYMELAEACEAE		
Drapetes tasmanicus	-	CC
Pimelea pygmaea	+	CC

APPENDIX (CONTINUED)

Species of Australasian cushion plants by family, including endemic status (+ = endemic; ++ = very restricted endemic) and cushion type (abbreviations as for Table 1)

FAMILY/SPECIES	ENDEMIC STATUS	CUSHION TYPE
NEW ZEALAND		
BORAGINACEAE		
Myosotis uniflora	+	SCp
M. pulvinaris	+	SCp?
CARYOPHYLLACEAE		
Colobanthus acicularis	+	SCp
C. brevisepalus	+	SCp
C. buchananii	+	SCp?
C. canaliculatus	+	SCp?
C. masonae	+	SCp
C. monticola	+	SCp?
C. wallii	+	SCp?
Scleranthus biflorus	-	FCp
S. brockiei	+	FCp
S. uniflorus	-	FCp
CENTROLEPIDACEAE		
Centrolepis ciliata	-	CoC
C. pallida	+	CoC
Gaimardia setacea	-	CoC
CYPERACEAE		
Carpha alpina[1]	-	CoC
Oreobolus pectinatus	+	CoC
O. impara	+	CoC
COMPOSITAE		
Abrotanella inconspicua	+	CoC
Celmisia argentea	+	CoC
C. sessiliflorus	+	CoC
Haastia pulvinaris	+	SCp
Raoulia australis	+	CC
R. bryoides	+	SCp
R. buchananii	+	SCp
R. eximea	+	SCp
COMPOSITAE (CONTINUED)		
Raoulia glabra	+	CC
R. goyenii	+	SCp
R. hectori	+	CC?
R. hookeri	+	CC
R. mammillaris	+	SCp
R. rubra	+	CC
R. subsericea	+	CC
R. subulata	+	CC
R. tenuicaulis	+	CC
R. youngii	+	FCp?
DONATIACEAE		
Donatia novae-zelandiae	-	CoC
EPACRIDACEAE		
Dracophyllum muscoides	+	SC
D. politium	+	SCp
HECTORELLACEAE		
Hectorella caespitosa	+	CoC
SCROPHULARIACEAE		
Chionohebe ciliolata	+	SCp
C. myosotoides	+	SCp
C. pulvinaris	+	SCp
C. thomsonii	-	SCp
STYLIDIACEAE		
Phyllachne colensoi	-	CoC
P. rubra	+	CoC
THYMELAEACEAE		
Drapetes lyallii	+	SCp
D. diefenbachii	+	CC
UMBELLIFERAE		
Anisotome imbricata var. imbricata	+	FCp?
AUSTRALIA (MAINLAND)		
CARYOPHYLLACEAE		
Colobanthus nivicola	+	SCp
C. pulvinatus	+	SCp
Scleranthus biflorus	-	SCp
CYPERACEAE		
Carpha alpina[1]	-	CoC
COMPOSITAE		
Ewartia nubigena	+	CC
EPACRIDACEAE		
Pentachondra pumila[2]	-	CC
LILIACEAE		
Astelia alpina[3]	-	CoC
PLANTAGINACEAE		
Plantago glacialis	+	CoC?
STACKHOUSIACEAE		
Stackhousia pulvinaris	-	CC
THYMELAEACEAE		
Drapetes tasmanicus	-	CC
MACQUARIE ISLAND		
CARYOPHYLLACEAE		
Colobanthus muscoides	-	SCp
UMBELLIFERAE		
Azorella selago	-	SCp
MOSS		
Ditrichum strictum	-	CM

APPENDIX (CONTINUED)

Species of Australasian cushion plants by family, including endemic status (+ = endemic; ++ = very restricted endemic) and cushion type (abbreviations as for Table 1)

FAMILY/SPECIES	ENDEMIC STATUS	CUSHION TYPE
NEW GUINEA		
BORAGINACEAE		
Trigonotis opaca	++	CoC
T. papuana	+	CoC
CARYOPHYLLACEAE		
Sagina donatoides	++	SCp
S. belanophylla	+	SCp
Scleranthus singuliflorus	-	SCp
CENTROLEPIDACEAE		
Centrolepis fascicularis	-	CoC
C. philippinensis	-	CoC
Gaimardia setacea	-	CoC
COMPOSITAE		
Abrotanella papuana	+	RC
Cotula leptoloba	+	CoC
C. sarawaketensis	++	CoC
C. wilhelminensis	++	CoC
Gnaphalium breviscapum	+	RC
Rhamphogyne papuana	+	RC
Tetramolopium pumilum	+	ShC
CYPERACEAE		
Carpha alpina	-	CoC
Oreobolus ambiguus	-	CoC
O. pumilio	-	CoC
ERICACEAE		
Rhododendron saxifragoides	+	ShC
Vaccinium ambylandrum	+	CC
V. oranjense	++	CC
ERIOCAULACEAE		
Eriocaulon alpinum	+	RC
E. batholithicola	++	RC
E. montanum	+	RC
E. novoguineense	+	RC
E. pioraense	++	RC
ERIOCAULACEAE (CONTINUED)		
E. pulvinatum	++	RC
E. scorpionensis	++	RC
E. tubiflorum	++	RC
GENTIANACEAE		
Gentiana crutwellii	++	CoC
G. papuana	+	CoC
ISOETACEAE		
Isoetes hopei	++	RC
LILIACEAE		
Astelia alpina[3]	-	CoC
MYRTACEAE		
Xanthomyrtus klossii	++	CC
PLANTAGINACEAE		
Plantago aundensis	+	RC
P. polita	+	RC
P. stenophylla	+	RC
POACEAE		
Danthonia oreoboloides	+	CoC
Poa callosa	+	CoC
P. clavigera	++	CoC
P. crassicaulis	+	CoC
P. inconspicua	++	CoC
P. papuana subsp. pulviniformis	++	CoC
RANUNCULACEAE		
Ranunculus sp.	++	CC
ROSACEAE		
Potentilla foersteriana var. brassii	++	RC
var. foersteriana	+	CC
UMBELLIFERAE		
Trachymene pulvilliforma	++	CC

[1] Carpha alpina forms cushions in New Guinea but only rarely in Tasmania, Australia and New Zealand
[2] Pentachondra pumila forms cushions in Australia but only rarely in Tasmania
[3] Astelia alpina forms cushions in New Guinea but only rarely in Australia and Tasmania

Hill, R.S. and Gibson, N. (1986) Macrofossil evidence for the evolution of the alpine and subalpine vegetation of Tasmania. IN Barlow, B.A. (ed) FLORA AND FAUNA OF ALPINE AUSTRALASIA. CSIRO, Melbourne.

CHAPTER TWELVE

MACROFOSSIL EVIDENCE FOR THE EVOLUTION OF THE ALPINE AND SUBALPINE VEGETATION OF TASMANIA

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INTRODUCTION

The macrofossil record of the Australian Tertiary vegetation in general is quite poorly documented, and in particular remains of alpine or subalpine plants are rare. There are isolated examples from the pollen record of alpine species from Tertiary sediments, but very little which assists in determining the origins of these vegetation types. However some Tertiary fossil-bearing sediments in Tasmania contain plant fragments which are comparable to extant alpine and subalpine species, and give some indication of the early development of the high altitude vegetation. The purpose of this paper is to consider the fossil history of some of the important elements of the alpine and subalpine vegetation and to comment on the past history of this vegetation.

MATERIAL AND METHODS

FOSSIL LOCALITIES

For ease of discussion the Tertiary sediments have been named after nearby towns or geographic features (Fig. 1). Detailed information is given on the age of the Monpeelyata flora since it is of particular interest in this paper. The localities are:

(1) Regatta Point: early Eocene (M.K. Macphail, pers. comm.).
(2) Hasties: middle to late Eocene (M.K. Macphail, pers. comm.).
(3) Cethana: middle Eocene to Oligocene (Hill 1984).
(4) Pioneer: Oligocene (Hill and Macphail 1983).
(5) Monpeelyata: The sediment containing the fossils is probably late Oligocene or early Miocene, and is unlikely to be less than 22 million years old. the evidence for this comes from two sources. Firstly, palynological data suggest that the sediment belongs to the Middle or Upper Proteacidites tuberculatus zone of Stover and Partridge (1974).

This is based on the presence of the following species and their known stratigraphic ranges in the Gippsland Basin (determinations by S. Forsyth, Department of Mines, Tasmania): Cyatheacidites annulatus, which makes its first appearance in the P. tuberculatus zone, Foveotriletes palaequetrus, which does not persist beyond the end of the P. tuberculatus zone, Nothofagidites flemingii and Periporopollenites demarcatus, which do not persist beyond the end of the Middle P. tuberculatus zone, and Polyadopollenites myriosporites, which makes its first appearance in the Upper P. tuberculatus zone. These pollen and spore occurrences strongly suggest that the sediment lies stratigraphically near the top of the Middle P. tuberculatus zone, which, according to Stover and Partridge (1974) approximates the Oligocene-Miocene boundary. Secondly, the fossil

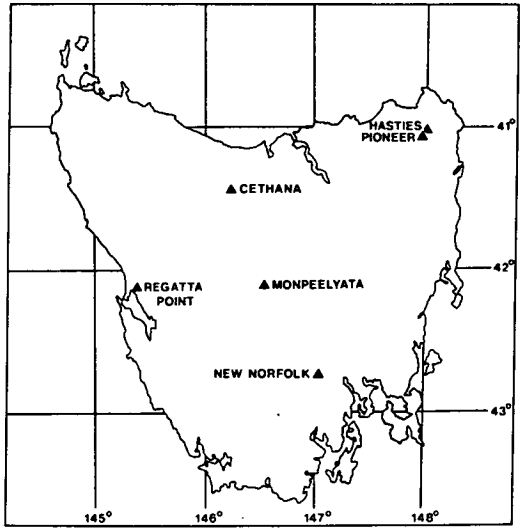


Fig. 1. Map of Tasmania showing the Tertiary localities. There are 2 deposits at Regatta Point

bearing sediment is capped by basalt. Although this particular basaltic outcrop has not been dated, 5 others in the Great Lake area have been, and their ages range from 23.6 to 21.8 million years (Sutherland et al. 1973). No basalts have been found on the Central Plateau which are less than approximately 22 million years old (early Miocene), which gives a probable minimum age for the fossil-bearing sediment which is in agreement with the palynological determination.

(6) Regatta Point: late Pliocene to early Pleistocene (Hill and Macphail 1985). This fossil-bearing sediment overlies the early Eocene sediment from the same locality mentioned above.

EXTANT LOCALITY

Leaf litter has been sampled intensively from the surface sediment of Lake Dobson, south central Tasmania, specifically for comparison with the Monpeelyata site (Hill and Gibson 1986). Lake Dobson is surrounded mostly by subalpine eucalypt woodland, with Nothofagus cunninghamii forming an intermediate understorey to a diverse microphyllous evergreen shrub layer. Sediment was collected at intervals along 3 transects and analyzed for leaves and reproductive structures.

TERTIARY VEGETATION HISTORY IN TASMANIA

LOWLAND VEGETATION

In order to understand the fossil record of alpine and subalpine vegetation in Tasmania it is important to first briefly consider the changes in lowland vegetation in Tasmania during the Tertiary. The Tertiary vegetation of lowland Tasmania can be reasonably well reconstructed using a combination of macro- and microfossil information. It should be remembered that plant fossilization is most likely to occur in high rainfall areas. Therefore the vegetation discussed below is biased in that direction. The extent of high rainfall areas in Tasmania during the Tertiary is not well documented.

There are at least 3 distinct phases in the Tertiary vegetation of Tasmania:

(1) In the early Tertiary subtropical vegetation was apparently widespread over Tasmania. For example, the early Eocene vegetation at Regatta Point consisted of a mangrove swamp dominated by the palm Nypa, with a forest containing Gymnostoma (tropical Casuarinaceae), Araucariaceae, Podocarpaceae and many broad-leafed angiosperms nearby. Similar elements, with the exception of Nypa, have been recovered from the middle to late Eocene Hasties flora. Both of these deposits are close to sea level, and represent examples of the lowland vegetation at the time. There are no reliable examples of high altitude floras which are contemporaneous with this lowland subtropical vegetation.

(2) In the middle Tertiary there was a mixture of subtropical and temperate vegetation in lowland Tasmania. The best example of this comes from the Oligocene Pioneer deposit. Geographically this deposit is very close to Hasties (Fig. 1), and it shows that the vegetation had changed substantially in the intervening time period. Temperate elements, and in particular Nothofagus, are dominant in both the macro- and microflora, but subtropical species are also present (e.g. Araucariaceae, Lauraceae) (Hill and Macphail 1983). The time of first appearance of temperate elements in Tasmania is unknown, but they are likely to have become a common part of the vegetation in late Eocene to early Oligocene times. There are 2 deposits of middle Tertiary age in Tasmania which probably represent high altitude vegetation, Cethana and Monpeelyata.

(3) By the late Tertiary the subtropical element had either disappeared from Tasmania or had been relegated to minor status. The late Pliocene-early Pleistocene Regatta Point flora contains a suite of plants

which are very similar to those in extant west coast Tasmanian rainforest (Hill and Macphail 1985).

HIGH-ALTITUDE VEGETATION

Two deposits in Tasmania are relevant to the evolution of the alpine and subalpine vegetation. The Cethana flora is probably the oldest, although the stratigraphic control on this site is poor. It could be as old as middle Eocene, which would make it contemporaneous with the early Tertiary subtropical lowland vegetation described above. However, it may be as recent as Oligocene, in which case it is contemporaneous with the middle Tertiary Pioneer flora. The Monpeelyata flora is middle Tertiary in age, and is probably more than 22 million years old.

The Cethana flora

The Cethana flora occurs at about 300 m elevation in north central Tasmania (Fig. 1). The geology of the area is complex and it is impossible at present to estimate its altitude at the time of deposition, although it is unlikely that it was significantly higher than at present. The flora is dominated by Nothofagus tasmanica, a species which is similar in leaf morphology to the extant N. moorei, which dominates temperate rainforest in northern New South Wales and southern Queensland. Other elements in the flora which have been described are N. cethanica, a species with leaves closely resembling the New Zealand endemic N. fusca, and N. gunnii (Hill 1984). The rest of the flora is undescribed, although some of the leaves can be confidently assigned to the Proteaceae, Myrtaceae and Cunoniaceae, and fronds of the fern genus Schizaea are also present.

The ecology of the living relatives of the Nothofagus species at Cethana suggests that the area may have been equivalent to an extant subalpine forest. Nothofagus fusca is associated with lowland and montane forests in New Zealand (Wardle 1984), and N. gunnii occurs as a tree in subalpine rainforest or as a shrub in exposed subalpine and alpine areas. The importance of N. tasmanica will be discussed later. The Cethana flora is dominated by microphyllous leaves (Table 1), which is also indicative of a cool climate.

The species diversity of this flora is relatively high, with more than 20 angiosperm species and several gymnosperms and ferns present. However, the distinctive families which produce extremely small evergreen leaves and which dominate much of the alpine and subalpine flora of Tasmania today are absent or uncommon (see Table 1 for comparison of leaf size with a typical extant subalpine vegetation).

It is probable that the fossils at Cethana are the remains of a cool temperate rainforest which contained at least 3 species of Nothofagus and a diverse tree and shrub component. Because of the current relatively low altitude of this site there are at least 3 hypotheses to explain the presence of elements which are now characteristic of high altitude areas (e.g. Nothofagus gunnii):

(1) These elements occurred in low altitude forests under relatively mild climatic conditions in the early to middle Tertiary and were later eliminated from these areas because of increasing competition from other angiosperms better adapted to the climate.

(2) These elements occurred in low altitude forests, but under a relatively cool climate which was similar to the extant subalpine climate.

(3) These elements were not part of the low altitude forest, but represent long distance dispersal from high altitude areas.

While hypothesis 3 is the least likely, there is not enough information available at present to refine these hypotheses.

The Monpeelyata flora

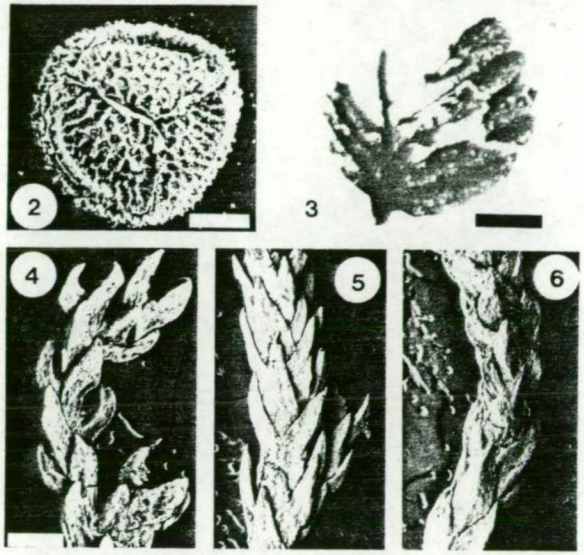
Monpeelyata is currently at about 920 m elevation and supports subalpine eucalypt woodland. It is probable that the altitude was similar at the time of deposition. The depositional site was probably a small lake, since the sediment is fine-grained and one of the common fossils is Isoetes (leaves and megaspores, Fig. 2). The Isoetes was probably in situ, as is commonly the case in subalpine and alpine lakes in Tasmania today. The presence of Nothofagus gunnii (Fig. 3) is also suggestive of alpine or subalpine conditions, and the microphyllous nature of the flora in general (Figs. 7-14) is indicative of the evergreen microphyllous shrubs which currently dominate at high altitudes in Tasmania. The comparison between the leaf size at Monpeelyata and the extant leaf litter collected in Lake Dobson, which is surrounded by subalpine eucalypt woodland, shows a remarkable similarity (Table 1), with the only major difference being that Lake Dobson contains some large leaves (eucalypts) which are apparently absent from Monpeelyata. It is probable that the vegetation at Monpeelyata was subalpine, since the discovery of a log approximately 30 cm in diameter indicates that it was below the treeline.

Table 1. Leaf length distribution from the Cethana and Monpeelyata localities, as % of each total sample. Data collected from leaf litter in Lake Dobson is included for comparison. Each sample is based on at least 150 leaves. As an indication of scale, Webb (1959) defined a microphyll as less than 7.6 cm long

LOCALITY	LEAF SIZE CLASS (CM)					
	0-1	>1-2	>2-3	>3-4	>4-4	>5
Lake Dobson	89.0	6.0	1.0	0.5	0.5	3.0
Monpeelyata	88.5	10.5	1.0	-	-	-
Cethana	4.9	21.1	26.8	21.9	9.8	15.5

Intensive collections of leaf litter at Lake Dobson (Hill and Gibson 1986) have shown that it is possible to reconstruct the composition of the vegetation surrounding the lake relatively well. The major problems are that the number of leaves deposited does not correlate well with dominance in the vegetation by a species, and unless a species is growing very close to the site of deposition (within about 5 m of the lake's edge) it is unlikely to occur as a macrofossil.

With these limitations in mind, a combination of the micro- and macroflora suggests that the common elements at Monpeelyata were N. cf. cunninghamii (Figs. 18, 19), a podocarpaceous species (Figs. 4-6), and a microphyllous angiosperm of unknown affinities (Figs. 7, 8). The pollen flora is dominated by Nothofagus brassii type pollen, but there are no macrofossils of this type present and it must be concluded that the pollen source plants did not grow in the vegetation surrounding the site of

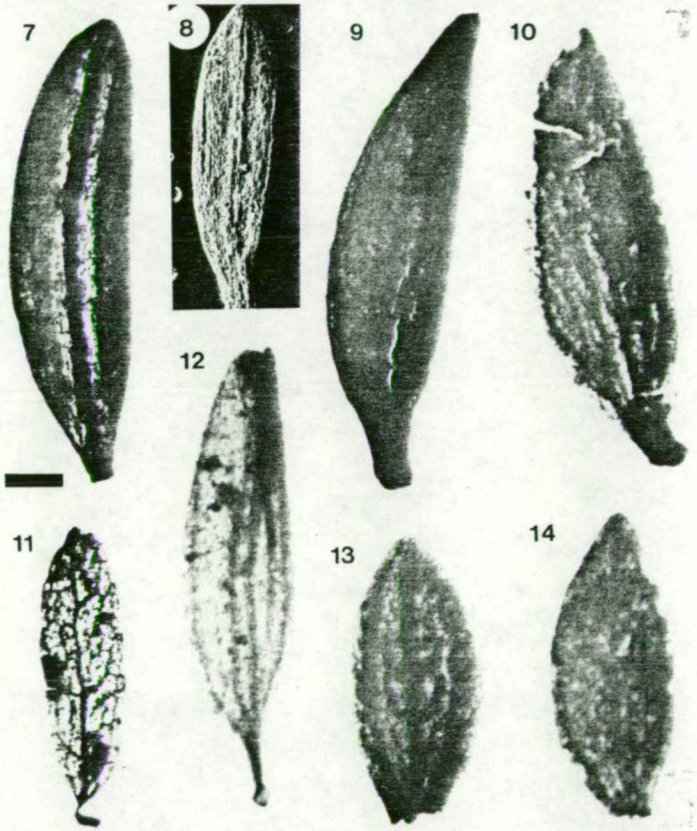


Figs. 2-6. 2, Scanning electron micrograph of an Isoetes megaspore from the Monpeelyata locality (scale = 0.1 mm). 3, Nothofagus gunnii leaf from the Monpeelyata locality (scale = 2 mm). The fossil leaf can be compared with the drawing of an adult N. gunnii leaf in Fig. 15. 4-6, Scanning electron micrographs of twigs belonging to the family Podocarpaceae from the Monpeelyata locality (scale = 1 mm).

deposition. Other macrofossils which have been identified include Nothofagus gunnii and Isoetes. There are a number of microphyllous angiosperm species present, and it is probable that they include at least one member of the Epacridaceae, which is also present in the pollen flora and as a single fruit, and possibly Myrtaceae.

It is significant that this middle Tertiary flora was deposited before Australia contacted the Sunda Plate, about 15 million years ago (Martin 1982). The flora is dominated by plants of Gondwanic origin, as is evidenced by the presence of Nothofagus and the families Podocarpaceae and

Epacridaceae. To date, no members of the cosmopolitan alpine flora have been identified from the macrofossil flora at Monpeelyata. One element which requires explanation is the family Araucariaceae, which is recorded as pollen and also possibly as a single cone scale. The Araucariaceae must have been an important feature of the early and middle Tertiary lowland vegetation of Tasmania (Bigwood and Hill 1985), but its presence in the cooler climates at higher altitudes requires explanation. Although



Figs. 7-14. Microphyllous leaves from the Monpeelyata locality (scale = 0.5 mm). Figs. 7 and 8 are transmitted light and scanning electron micrographs respectively of the dominant microphyllous leaf in the flora

most extant araucarians are subtropical or tropical, Araucaria araucana is found in association with the winter deciduous species Nothofagus antarctica and N. pumilio at high altitudes in Chile (Veblen and Schlegel 1982; J. Read, pers. comm.), and a similar situation may have occurred at Monpeelyata.

One of the most important features of the Monpeelyata flora is that it shows that the plants of Gondwanic origin which currently occur in alpine and subalpine areas of Tasmania probably have a very long history in such environments, extending back at least 22 million years. Therefore in Tasmania at least there was probably a well developed and well adapted subalpine flora in place before contact with the Sunda plate allowed access for the cosmopolitan element into these areas.

TERTIARY HISTORY OF NOTHOFAGUS IN TASMANIA

One of the most important genera in the Tasmanian vegetation is Nothofagus. There are currently 2 species of Nothofagus in Tasmania, and both are represented in the fossil record. Nothofagus cunninghamii is a dominant tree in lowland cool temperate rainforest, but it occurs as a shrub in the alpine and subalpine zone. The winter-deciduous N. gunnii occurs in tree form in subalpine rainforest and as a shrub in exposed alpine and subalpine situations. The fossil record of both species consists almost entirely of leaves, although occasionally fruits are also found. Leaves are particularly useful, since leaf morphology is sensitive to changes in climate, and therefore may accurately reflect changing conditions through time.

NOTHOFAGUS GUNNII

Nothofagus gunnii macrofossils have been recovered from only 2 localities, Cethana and Monpeelyata (Fig. 3). The N. fusca type pollen, which is produced by N. gunnii has been present in Australia since the Palaeocene (Muller 1981), and the macrofossils clearly post-date this. The striking feature of the fossil leaves, which are at least 22 million years old, is that they are indistinguishable morphologically from extant N. gunnii leaves. This suggests that this species has a very long and stable history, and may have been one of the first angiosperms to grow at high altitudes in Tasmania. The leaves of N. gunnii are very similar in morphology to the Chilean N. pumilio, which occupies similar habitats. This similarity is even more striking when it is seen that N. gunnii produces a range of juvenile leaves, one of which exhibits the same venation pattern as adult N. pumilio leaves (Hill 1984) (Fig. 15). It is probable that N. gunnii and N. pumilio had a common ancestor which migrated from South America and reached Australia in the early Tertiary. Truswell (1982) believes that the coastal Antarctic environment of the early Tertiary would have been suitable for the growth and reproduction of this type of Nothofagus.

NOTHOFAGUS CUNNINGHAMII

Every post-Eocene deposit in Tasmania which has been investigated contains a very high proportion of leaves which can be described as Nothofagus cunninghamii-type. The N. menziesii-type pollen, which is produced by N. cunninghamii, has an Australian record extending back to the early Eocene (Muller 1981), but Eocene macrofloras appear to be dominated by subtropical plants at the expense of the temperate element. It may be that the temperate species (including the Nothofagus cunninghamii type) were present in the Eocene but were in restricted niches. The Cethana flora may represent an example of this.

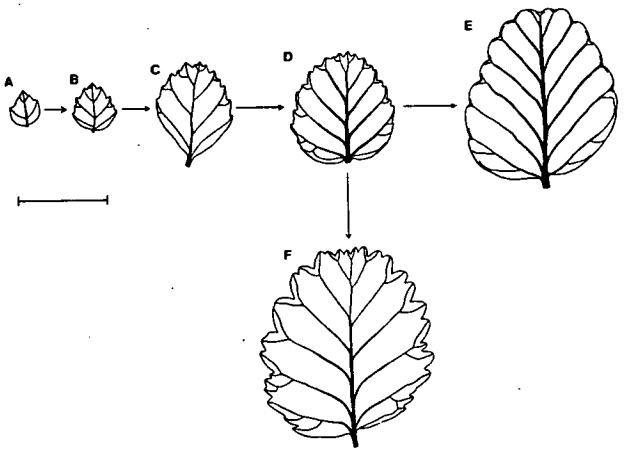


Fig. 15. A-E, Drawings of the series of leaves produced by Nothofagus gunnii following germination. Fig. 15,E represents the typical adult foliage. F, Adult leaf of N. pumilio, which is very similar in venation pattern to the juvenile N. gunnii leaf shown in D. Scale = 1 cm

The line of Nothofagus which led to extant N. cunninghamii exhibits a progressive change in leaf morphology through the Tertiary which was summarized by Hill (1983). In essence, the oldest leaves resemble extant N. moorei in size and morphology, and there is a gradual change in leaf size and morphology until the Late Tertiary when the fossil leaves are indistinguishable from extant N. cunninghamii leaves.

The information provided by Hill (1983) contained a large time gap between the Oligocene and the late Pliocene which can now be partially filled by the Monpeelyata flora. The cooler climate at Monpeelyata

appears to have had an important effect on evolution in this line of Nothofagus, which can be demonstrated in two ways. Firstly, as mentioned earlier, there is a change in leaf size through the Tertiary in these Nothofagus leaves, which in general is manifested by a gradual reduction in both length and width (Fig. 16). However, the Monpeelyata leaves are within the size range exhibited by extant N. cunninghamii, and as such appear to be out of sequence with the general trend. Since it is probable that the reduction in leaf size through the Tertiary is at least partially in response to decreasing temperatures, the most likely explanation for the small leaf size at Monpeelyata is that the species was responding to the cold conditions at a high altitude.

The second way in which evolution of Nothofagus has apparently been affected by the more extreme climate at Monpeelyata is through changes in leaf morphology. There is a large size range in Nothofagus leaves at Monpeelyata and there is a corresponding range of morphology. The larger leaves resemble N. moorei in serration type and vein pattern, while the smaller leaves resemble N. cunninghamii in these features (Figs. 17-20). This is the earliest example of N. cunninghamii leaf morphology in the

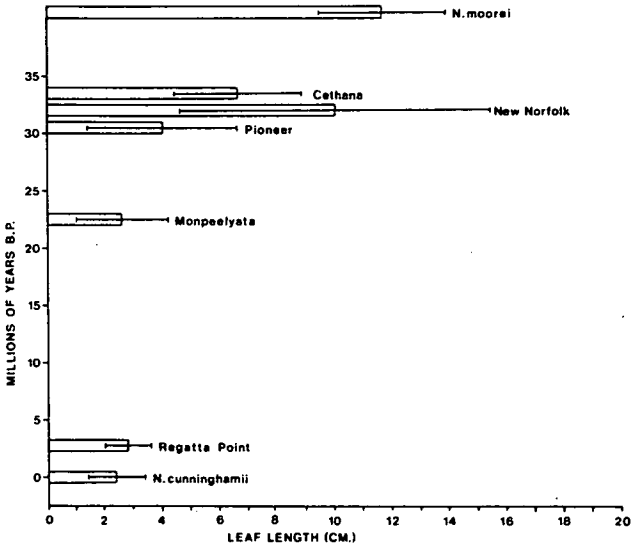
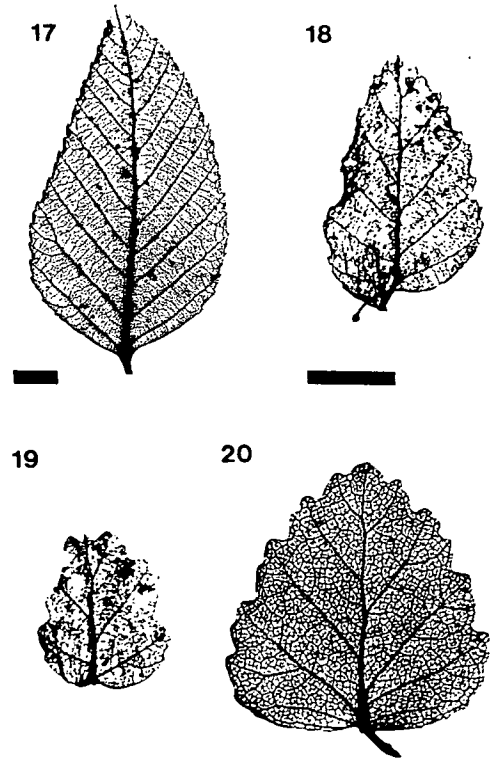


Fig. 16. Leaf lengths and standard deviations of Nothofagus leaves from Tertiary localities in Tasmania. Extant N. moorei and N. cunninghamii are shown at the top and bottom respectively. All leaves belong to the group described by Hill (1983) as linking N. moorei and N. cunninghamii. The age of each deposit is depicted as the mid-point of its stratigraphic range

fossil record, and it may be that the cooler high altitude climate accelerated the change in morphology leading to this leaf type.

It is notable that although the average leaf length of the Monpeelyata Nothofagus leaves is about the same as extant N. cunninghamii (Fig. 16), the leaves are actually much smaller in area because the larger leaves are relatively narrow. Therefore if leaf size was expressed as leaf area, the Monpeelyata Nothofagus leaves would be significantly smaller than extant lowland N. cunninghamii.

Therefore the history of the two Nothofagus species in Tasmania is



Figs. 17-20. **17**, Cleared leaf of extant Nothofagus moorei (scale = 5 mm). **18,19**, Nothofagus leaves from the Monpeelyata locality. Note the similarity of the serration types and venation patterns to N. moorei (Fig. 17) and N. cunninghmamii (Fig. 20) respectively. Scale = 5 mm. **20**, Cleared leaf of extant N. cunninghamii (scale as for Fig. 18)

quite different. Nothofagus gunnii has a long and stable history, and it may have been a part of the high altitude vegetation of Tasmania throughout its time there. On the other hand, N. cunninghamii exhibits a clear change in morphology during the Tertiary, beginning as a relatively large leaved species and gradually reducing in size and changing in morphology probably in response to decreasing temperatures.

Macrofossil evidence from Tasmania suggests that cold-adapted floras were in place by at least 22 million years ago. While there is no evidence of treeless vegetation, the Monpeelyata flora and to some extent the Cethana flora contain species which are similar taxonomically and physiognomically to extant alpine species in Tasmania. These species would have adapted quickly to the alpine conditions which developed in Tasmania in the late Tertiary.

ACKNOWLEDGMENTS

We thank Mr S. Forsyth and Dr M. Macphail for palynological determinations and Ms J. Read for critically reading the manuscript. This research was supported by the ARGS.

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TETRATHECA GUNNII HOOK. F. ON SERPENTINE SOILS NEAR BEACONSFIELD, TASMANIA

by M.J. Brown, H.J. Bayly-Stark, F. Duncan and N. Gibson

(with one table and two text-figures)

BROWN, M.J., BAYLY-STARK, H.J., DUNCAN, F. & GIBSON, N., 1986 (12:ix): *Tetratheca gunnii* Hook. f. on serpentine soils near Beaconsfield, Tasmania. *Pap. Proc. R. Soc. Tasm.* 120: 33-38. ISSN 0080-4703. National Parks and Wildlife Service, Sandy Bay, Tasmania 7005.

The rediscovery of *Tetratheca gunnii* Hook. f., a species last collected in 1843 and presumed extinct, is reported. The morphological variability among plants (including previously undescribed fruit) is given to facilitate comparison with descriptions of the type material. The habitat of the species is described and options for management to conserve viable populations are discussed.

Key Words: ***Tetratheca gunnii*, serpentine, Tasmania, conservation.**

INTRODUCTION

This paper reports the rediscovery of *Tetratheca gunnii* Hook. f., a species previously known only from the type and one duplicate collection made by R. C. Gunn in 1843 (Hooker 1855, in Thompson 1976). In their census of extinct and endangered Australian plants, Leigh *et al.* (1984) categorised *T. gunnii* as "presumed extinct". Leigh *et al.* (loc. cit.) and Thompson (loc. cit.) have emphasized the need to relocate the species, so that its specific status can be verified and appropriate conservation measures can be undertaken.

THE STUDY AREA

The holotype of *T. gunnii* was collected from the foothills of the Asbestos Range on serpentine rocks. The Asbestos Range and associated Dazzler Range form a dissected upland between the Tamar River (Port Dalrymple) and Port Sorell, reaching an altitude of 520 m. The ranges are located in the moist subhumid and humid warm climatic zones respectively (Gentilli 1972). The area is geologically and topographically complex (Gee & Legge 1971) and supports a range of vegetation types from rainforest through eucalypt forest to heath (Brown & Buckney 1983, Kirkpatrick & Dickinson 1984).

The search for *Tetratheca gunnii* was concentrated on the Cambrian serpentinite, peridotite and associated ultramafic rocks which crop out locally in undulating terrain in the eastern foothills of the Dazzler Range, about 3 km west of Beaconsfield (fig. 1). The range of altitudes of these rocks is 20 to 220 m. The vegetation mainly comprises dry

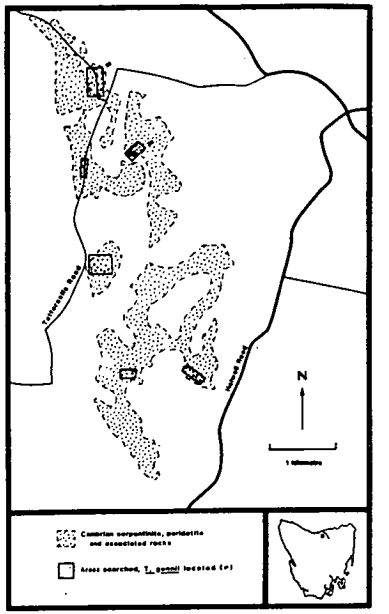

FIG.1 — Map showing distribution of serpentine soils, areas searched and locations of T. gunnii.

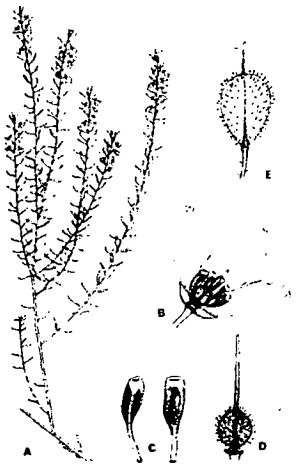

FIG. 2 — Tetratheca gunnii: *(a) habit of flowering specimen, x0.75; (b) flower with one sepal, one petal and three stamens removed, x7.5; (c) stamens, x15; (d) ovary and style, x15; (e) fruit, x7.5.*

sclerophyll forest with a heathy or shrubby understorey. Shafts, scrapes and spoil heaps are common in the serpentinite area, which was worked previously for asbestos and more recently for chromite. Other land uses in the immediate area are logging for pulp, sawlogs and firewood, grazing, clearing, gravel extraction and protection of water quality (water reserve).

The area was searched by the authors on 3 October 1985 when the initial findings were made. The area was revisited on 19 December 1985 to obtain fruiting material for description and seed for propagation by the Royal Tasmanian Botanical Gardens. Specimens are lodged with the Tasmanian Herbarium (HO).

RESULTS AND DISCUSSION

Occurrence and Habitat

Plants were found growing on shallow soils at four distinct locations in two of the six areas searched (fig. 1). All of the sites were underlain by serpentine rocks (Gee & Legge 1971). A total of 24 individuals were found with 20 in one population, two in another and the remaining two plants occurring as solitary individuals. In each case, the plants were found growing on gently sloping hillsides of east to southeast aspect in heathy *Eucalyptus amygdalina* woodland (Duncan & Brown 1985). *Eucalyptus amygdalina* is the overstorey dominant, with *E. ovata* present as a minor species. *Casuarina littoralis* and *Banksia marginata* form a small tree-tall shrub stratum over a dense heath dominated by *Epacris virgata*, *Correa reflexa* and *Hibbertia riparia*. Cutting grass (*Gahnia* spp.), grasses, saggs and procumbent shrubs are also widespread. Species lists for each site are given in appendix 1.

At each location, *T. gunnii* is closely associated with two other endemic species, also largely restricted to serpentine rocks, viz. *Epacris virgata* and *Spyridium obcordatum* (Kirkpatrick & Brown 1984). However, the latter two species are much more abundant. Serpentine rocks worldwide are noted for their high local endemicity (e.g. Whittaker 1954, Kruckeberg 1954) and those near Beaconsfield appear to be no exception.

Kruckeberg (1954) presented evidence that serpentine endemics are unable to compete with non-serpentine species in comparatively dense closed communities. The very pronounced boundaries of the *Epacris virgata* population indicate that this species is a serpentine endemic. *Spyridium obcordatum* is strongly associated with serpentine rocks, but does occur albeit rarely, on other rock types (Brown *et al.* 1983) and may represent an example of biotype depletion (Stebbins 1942). *Tetratheca gunnii* has only been found on serpentine rocks and may be a serpentine endemic. It exhibits "serpentomorphic" characteristics (Whittaker 1954) as compared with its close congener *T. pilosa*. The latter species occurs with *T. gunnii* on this rock type but is found more widely in other edaphic situations. The ecological and genecological status of *T. gunnii* can only be confirmed by further investigations.

Description

In most respects, the plants found in the present study fit closely to the description of *T. gunnii* given by Thompson (1976). The absence of an anther tube is particularly distinctive (fig. 2) and immediately separates the species from *T. pilosa* and from the morphologically similar *T. procumbens* Gunn ex Hook. f. (which is included in *T. pilosa* by Thompson *loc. cit.*).

TABLE 1

Morphometric Data for *Tetratheca gunnii*. Mean Value (and ranges) in mm.

	Site	Site 2	Sites 3 and 4				
			P1	P2	P3	P4	Mean
Leaf length (blade)	5.4 (5.2-5.8)	3.5 (3.0-3.8)	5.1 (4.2-5.8)	4.1 (3.8-4.5)	5.2 (4.8-5.8)	4.6 (3.6-5.5)	4.65
Leaf width (max)	1.0 (0.9-1.0)	0.9 (0.7-1.2)	1.1 (0.9-1.2)	1.1 (0.9-1.4)	1.0 (0.9-1.1)	0.9 (0.6-1.1)	1.0
Petal length	3.4 (3.0-4.2)	2.6 (2.2-3.2)	5.2 (4.6-5.7)	4.5 (4.0-5.2)	4.5 (4.0-4.8)	3.5 (3.3-3.9)	4.0
Sepal length	1.0 (1.0-1.0)	0.9 (0.9-1.0)	1.3 (1.2-1.3)	1.0 (1.0-1.1)	1.0 (1.0)	1.1 (1.0-1.1)	1.05
Stamen length	2.1 (2.0-2.2)	1.4 (1.2-1.6)	2.6 (2.5-2.7)	2.4 (2.3-2.4)	2.3 (2.1-2.4)	1.9 (1.8-2.2)	2.1
Peduncle length	3.6 (3.2-4.3)	2.4 (2.1-2.6)	2.3 (1.5-2.7)	2.4 (1.9-2.7)	2.7 (2.4-3.1)	2.3 (2.3)	2.6
Style length	1.6 (1.4-1.8)	1.3 (1.2-1.5)	2.1 (2.0-2.1)	1.9 (1.8-2.0)	2.0 (2.0)	2.0 (1.9-2.0)	1.8
Stem width (internodal in flowering section)	0.6 (0.6)	0.7 (0.7)	0.7 (0.7)	0.6 (0.6)	0.7 (0.7)	0.7 (0.7)	0.7

Plants are generally lax and less than 0.3 m tall, but one individual was erect to 0.8 m. The plants are smaller in all their parts than *T. pilosa* especially in comparison with the robust forms of the latter which grow in the same area. Table 1 gives some morphometric data from six plants of *T. gunnii* to indicate variability between plants.

The petals vary in colour from pale lilac to deep pink-purple. Thompson (*loc. cit.*) suggests that the petals are usually white, but no white flowered specimens were seen. However, flowers on some specimens did fade within a few days of collection.

The fruit is a compressed 2(-3) locular capsule, obovate to cuneate, turgid 4.0 mm long, 2.5-3.0 mm wide, with uniform cover of sparsely scattered gland-tipped hairs. Slightly channelled along septum, style not persistent, opening along margin.

Seeds are pale, 3.0 mm long, almost oblong, covered with fine, appressed to spreading hairs, appendage pale covered with finer hairs. Similar to *T. pilosa* but base not scarred.

Conservation and Management

It seems likely that the serpentine provides the only suitable habitat for *T. gunnii*, and its distribution is very restricted even on this geological type. The serpentine rocks in the area occupy 530 ha, of which 270 ha (51%) is State Forest, 220 ha (41%) is privately owned and 40 ha (8%) is Crown Water Reserve. All of the *T. gunnii* plants found were in State Forest.

The main risks to survival for the species appear to be land clearing, adverse firing and grazing regimes and overcollecting. Some of the private land in the area has been cleared to rough pasture, to the detriment of *Epacris virgata* and *Spyridium obcordatum*, and further clearing for agriculture and for gravel extraction are potential threats. There is good evidence that grazing by introduced stock and frequent firing on State Forest in the area were also detrimental to the above species in the past. There has been a dramatic increase in the abundance and vigour of *E. virgata* on some previously grazed sites following recent cessation of grazing. Duncan (1981) has shown that *Tetratheca glandulosa* (= *T. labillardieri* Thompson) is dependent on seed for regeneration following a hot fire. If the same applies to *T. gunnii*, then fire regimes suitable for the maintenance of the populations will have to be determined.

The serpentine areas on State Forest generally support poor stands of timber, and are unlikely to

be clearfelled. Clearing of tracks for timber, mining or gravel extraction may not pose a direct threat to the species. However there remains the problem of possible introduced pathogens. The effects of *Phytophthora cinnamomi* on serpentine soils in general and *T. gunnii* in particular are unknown. Other species of *Tetratheca* are very susceptible to attack, but no symptoms consistent with *P. cinnamomi* infection were evident in the area. Soils in the area have been tested previously, but no *P. cinnamomi* was recovered.

The occurrence of *T. gunnii* in such close association with other restricted endemic species, confers on the area a very high significance for biological conservation. It is essential that a monitoring programme be established to continually review the status of *T. gunnii*, which has now been confirmed as an extant but endangered species.

ACKNOWLEDGEMENTS

We wish to thank S.J. Jarman, A.E. Orchard and N.J. Turner for their comments on the draft manuscript. The survey was undertaken during projects funded by the Australian Heritage Commission (FD), the Australian National Parks and Wildlife Service and the Tasmanian Forestry Commission (NG).

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(accepted Nov. 27, 1985)

APPENDIX 1

List of Vascular Species Associated with *Tetratheca gunnii* Hook. F. Near Beaconsfield.

A comprehensive list of species is given below for each *T. gunnii* site. Species were recorded from a circular plot of a nominal 15 m radius, which was centred on each population of *T. gunnii*. Except where indicated, species authorities are those given by Brown *et al.* (1983) for endemics, Curtis (1963, 1967) and Curtis and Morris (1975) for other dicotyledons, and Willis (1970) for other monocotyledons and pteridophytes. Endemic species are prefixed by an 'e', introduced species by an 'i', and poorly reserved species (Brown *et al.* 1983) by an 's'. Abundance of each species on each site is indicated by: + = uncommon; o = occasional; a = abundant and/or dense. The numbers of *T. gunnii* recorded from each site are: site 1 one plant; site 2 — one plant, site 3 — two plants, site 4 — twenty plants.

			SITE			
			1	2	3	4
PTERIDOPHYTES						
Aspleniaceae		*Asplenium flabellifolium*	+			
Dennstaedtiaceae		*Pteridium esculentum*	+	o	+	o
Lindsaeaceae		*Lindsaea linearis*	+			+
Sinopteridaceae		*Cheilanthes tenuifolia*	+			
DICOTYLEDONS						
Asteraceae		*Craspedia glauca*	+			
		Gnaphalium sp.	+			
		Helichrysum dendroideum	+	+		
		Helichrysum scorpioides	+	+	+	+
	i	*Hypochaeris radicata*		+		
		Olearia erubescens			+	
		Olearia lirata	+			
		Olearia ramulosa		+		
Campanulaceae		*Wahlenbergia* sp.	+			+
Casuarinaceae		*Casuarina littoralis*	a	a	a	a
Dilleniaceae		*Hibbertia riparia*	a	a	a	a
Droseraceae		*Drosera auriculata*	+		+	
Epacridaceae		*Acrotriche serrulata*	o	+	+	o
		Astroloma humifusum	a	o	o	o
		Epacris impressa	o	+	o	o
	e,s	*Epacris virgata*	a	a	a	a
		Styphelia adscendens		+	+	
Fabaceae		*Bossiaea prostrata*	o	+	+	
		Hovea heterophylla	+	+		
		Pultenaea stricta				
Goodeniaceae		*Goodenia lanata*	o	+	+	o
Haloragaceae		*Gonocarpus tetragynus*	o	o	+	+
		Gonocarpus teucrioides		+		o
Lauraceae		*Cassytha glabella*	+	+		
		Cassytha pubescens				+
Mimosaceae		*Acacia dealbata*		o		
		Acacia melanoxylon	+			
		Acacia mucronata			+	
Myrtaceae		*Acacia verticillata*		o		
		Baeckea ramosissima			o	o
	e	*Eucalyptus amygdalina*	a	a	a	a
		Eucalyptus ovata	o	o	o	o
		Leptospermum scoparium		+		
Oleaceae		*Notelaea ligustrina*		+		
Oxalidaceae		*Oxalis corniculata*			+	
Pittosporaceae		*Bursaria spinosa*			o	+
Polygalaceae		*Comesperma volubile*	o	+	+	+
Proteaceae		*Banksia marginata*	a	a	a	a
	e	*Hakea epiglottis*				+
	e	*Lomatia tinctoria*	o	o	+	o
Rhamnaceae	e	*Pomaderris elliptica*			a	
		Pomaderris pilifera				+
	e,s	*Spyridium obcordatum*	a	+	o	a

APPENDIX 1

List of Vascular Species Associated with *Tetratheca gunnii* Hook. F. Near Beaconsfield.

			SITE			
			1	2	3	4
Rubiaceae		Galium australe			+	
Rutaceae		Correa reflexa	a	a	a	a
		Zieria arborescens				+
Santalaceae		Exocarpos cupressiformis	+	+	o	a
Stackhousiaceae		Stackhousia monogyna			+	
Stylidiaceae		Stylidium graminifolium	+			
Tremandraceae	e,s	Tetratheca gunnii	+	+	+	o
		Tetratheca pilosa	+			o
Thymelaeaceae		Pimelea humilis	o	+		
		Pimelea nivea			+	o
Violaceae		Viola hederacea	+	o	+	+
MONOCOTYLEDONS						
Cyperaceae		Gahnia grandis	+	+	o	a
		Gahnia radula		o	+	+
		Lepidosperma elatius		o		
		Lepidosperma laterale	+	+	o	+
	e	Lepidosperma lineare var.inops	o		+	+
		Schoenus apogon			+	+
Liliaceae		Arthropodium milleflorum		+		
		Dianella revoluta			+	
Orchidaceae		Acianthus exsertus			+	
		Chiloglottis sp.	+		+	+
		Glossodia major			+	
		Pterostylis longifolia			+	
		Pterostylis nutans	+	+	+	+
		Thelymitra sp.		+		
Poaceae		*Deyeuxia quadriseta*	+	+		
		Microlaena stipoides	+	o	+	
		Poa sieberana Spreng.	o	o	+	+
	e	*Stipa aphylla*	o	o	o	+
		Tetrarrhena distichophylla	+	+	+	
		Themeda australis	+	o		
Xanthorrhoeaceae		*Lomandra longifolia*	o	o	o	o

Australian Journal of Ecology (1985) **10**, 91–99

Vegetation and flora associated with localized snow accumulation at Mount Field West, Tasmania

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Abstract

The vegetation associated with a snow patch at Mt Field in Tasmania is described and mapped. Seven distinct vegetation types were found to be related directly to topography and hence to the patterns of snow accumulation, snow melt and soil drainage. The fjaeldmark found where snow lies longest is unusual for Tasmania and may be the product of past climatic events and a peculiar parent material. At the generic level there exists a high similarity with the snow patch flora of the Australian Alps.

Introduction

Although there is a large literature exploring the alpine vegetation associated with prolonged snow accumulation in the northern hemisphere (e.g. Holaway & Ward 1963; Billings & Bliss 1959; Flock 1978; Bell & Bliss 1979; Helm 1982, Miller 1982) relatively little information is available from the southern hemisphere (Costin 1954; Billings & Mark 1961; Mark & Bliss 1970; Archer *et al.* 1973) where there have been no detailed studies of the vegetation and environment of single snow patches. The maritime nature of the Tasmanian climate precludes extensive areas of prolonged snow lie (Kirkpatrick 1982, 1983), making the vegetation of the few lee slopes on which snow accumulation does occur of considerable interest (Kirkpatrick & Harwood 1980).

In this paper we describe and analyse the vegetation of a snow accumulation area on Mt Field West, Tasmania, and correlate vegetation patterns with snow lie, topograhic position, soil characteristics and imputed moisture availability.

The study area

The snow patch occurs at approximately 1200 m above sea level, 60 m above the highest altitude of tree growth locally. The parent material is Permian mudstone and sandstone, an unusual occurrence within the Jurassic dolerite making up the rest of the Mt Field massif (42° 41′S, 146° 30′E). The snow patch occurs in the easterly lee of the ridge forming the local westerly extreme of the alpine environment.

There are no precipitation data available for the study area. However, data from the nearest climatic stations suggest that the mean annual precipitation almost certainly exceeds 2500 mm with a strong winter maximum and without any month, on average, receiving less than 50 mm. Snow, while being most frequent in late winter and early spring, can fall at any time of the year. Snow fall and persistence are highly variable. Winds frequently reach gale force. The major large herbivore is the Bennets wallaby.

Methods

The extent of the snow patch was monitored monthly from two photopoints as it receded during the winter, spring and early summer of 1982. In January 1983 topography and vegetation boundaries were surveyed using a dumpy level and Carr staff. Vegetation units were discriminated for mapping by structure and lifeform dominance. Soil samples were collected from three of the major perceptible types for later analysis.

Three topographically surveyed transects were laid out parallel to the slope, such that they passed through most of the mapped vegetation types (Fig. 1). The transects consisted of 35 x 35 cm contiguous quadrats within which were recorded the cover of plant taxa, rocks and bare ground, and the number of scats. Estimation of cover was aided by the division of the quadrat into 49 equal parts. Ten extra quadrats were laid out randomly in *Abrotanella forsteroides* bolster heath, a vegetation type missed by the transect sampling, making a total of 300 quadrats.

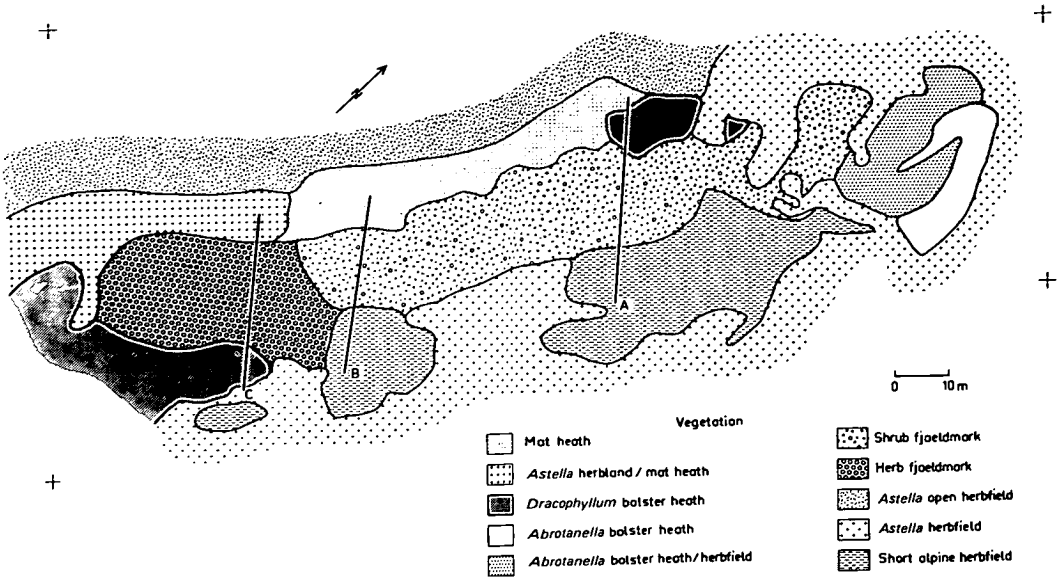

FIG. 1. Vegetation map of snowpatch at Mt Field, Tasmania. Position of transects, A, B, C are indicated.

Species presence data from the quadrats were classified using a monothetic divisive procedure based on the information statistic (Williams *et al.* 1966), and were ordinated using detrended correspondence analysis (Hill & Gauch 1980). Structural nomenclature follows Kirkpatrick (1983) except that a community with large shrubs and much bare ground is denoted as shrub fjaeldmark. Species nomenclature follows Curtis (1963, 1967), Curtis and Morris (1975), Curtis and Stone (1978) and Costin *et al.* (1979).

Results

Numerical analysis of quadrat data

At the seven group level of division there was a strong correspondence between the structural vegetation types perceived in the field and those recognized by the classificatory analysis (Table 1).

The short alpine herbfield (Figs 1–3) divided into two floristically defined groups which appear to correspond to the upper (group 1) and lower (group 3) occurrences of this vegetation type (Table 1).

Transect B ran along the major drainage line of the lower herbfield. *Ranunculus triplodontus, Scirpus subtilissimus, Agrostis* sp., and *Caltha phylloptera* exhibited high constancy and fidelity to the group (3) confined to this area (Table 2), the group being defined by the absence of *Drosera arcturi* and *Schoenus calyptratus* and the presence of *Ranunculus*.

Transect A cut across the slope of the upper herbfield. The most faithful and constant taxa in the group (1) confined to this area are *Carex hypandra* and *Erythranthera australis* (Table 2). This group was defined by the presence of *Drosera arcturi* and *Carex hypandra*. The vegetation in groups 1 and 3 is composed almost entirely of graminoids, herbs and moss (Table 1).

Group 4, characterized by the joint presence of *Gnaphalium traversii* and *Drosera arcturi*, is transitional between the short alpine herbfield communities and the fjaeldmark communities (Table 1 and 2).

Herb and shrub fjaeldmark were distinguished by the classificatory analysis. The herb fjaeldmark (group 5) differs structurally from the shrub fjaeldmark (group 6) in its relative lack of shrubs and bare ground and in its relative abundance of herbs and moss (Table 1). Neither the herb fjaeldmark nor the shrub fjaeldmark have any species that could be considered both highly faithful and constant. Group 5 is defined by the presence of *Schoenus calyptratus* and the absence of *Drosera arcturi* and lichens. Group 6 is characterized by the absence of *Drosera arcturi, Schoenus calyptratus* and *Ranunculus triplodontus*, the species with the highest percentage

TABLE 1. Analysis of the classification of combined transect data by life form (% overlapping cover) and a comparison of vegetation units perceived in the field and by classification

	Classification units						
	3	1	4	5	6	7	2
Number of quadrats	31	31	16	58	69	45	35
Average cover bare ground	3.6	0.4	18.9	25.4	49.5	2.7	13.1
Average cover of bolster shrubs	0.0	0.0	2.9	0.0	0.0	66.3	0.4
Average cover of mat shrubs	0.0	0.0	0.0	0.2	0.2	0.2	34.1
Average cover of tall shrubs	0.0	0.0	0.8	7.2	16.8	1.2	5.5
Average cover of graminoids	70.5	105.3	39.0	9.6	7.3	8.9	21.8
Average cover of *Astelia*	0.0	3.6	0.0	11.5	21.8	15.1	10.8
Average cover of forbs	57.5	23.8	14.0	20.4	7.8	6.4	10.1
Average cover of lichen	0.0	0.0	0.2	0.0	0.3	4.1	3.0
Average cover of moss	9.3	13.8	30.7	26.5	2.9	2.3	1.7
Average number of scats	4.3	2.1	0.8	1.1	1.1	1.4	1.6
Quadrats in mat heath (%)	–	–	–	1.7	7.2	–	57.1
Quadrats in *Astelia* herbfield/mat heath (%)	–	–	–	19.0	1.4	–	–
Quadrats in shrub fjaeldmark (%)	–	–	50.0	17.2	75.4	4.4	28.6
Quadrats in herb fjaeldmark (%)	–	–	31.3	50.0	11.6	–	–
Quadrats in *Dracophyllum* bolster heath (%)	–	–	12.5	3.4	1.4	73.3	14.3
Quadrats in *Abrotanella* bolster heath (%)	–	–	–	–	–	22.2	–
Quadrats in short alpine herbfield (%)	100.0	100.0	6.3	8.6	2.9	–	–

Fifteen quadrats in which no vegetation was found were excluded from the analysis.

frequencies in this group being *Poa gunnii* and *Helichrysum backhousii*. Both groups showed a high percentage of bare ground (Table 1).

Group 7 is the bolster heath communities which are characterized by the high fidelity and constancy of *Dracophyllum minimum* and *Mitrasacme archeri*, and defined by the presence of *Drosera arcturi* and the absence of *Carex hypandra* and *Gnaphalium traversii*.

Group 2, defined by the absence of *Drosera arcturi* and the presence of *Schoenus calyptratus* and lichens, and best characterized by lichens, *Pentachondra pumila* and *Celmisia longifolia* (Table 2), includes mat heath and a mixture of shrub fjaeldmark and *Dracophyllum* bolster heath.

Environmental relationships of the major vegetation types

The major environmental relationships between the groups were investigated using the indirect ordination technique detrended correspondence analysis (Hill & Gauch 1980; Fig. 4). Axis 1 is closely related to the imputed moisture availability during summer, with the two herbfield communities (1 and 3) falling at one extreme. These communities occur on areas of

FIG. 2. Lower short alpine herb field from upper short alpine herb/shrub fjaeldmark boundary. Herb fjaeldmark can be seen in the distant right above the herbfield.

FIG. 3. Upper short alpine herbfield from creek line at the bottom of the shrub fjaeldmark. *Astelia* tall alpine herbfield at the right of the creek.

TABLE 2. Percentage frequency of species by classificatory group

	Groups						
	3	1	4	5	6	7	2
Ranunculus triplodontus	100.0		6.3				
Scirpus subtilissimus	83.9	6.5	12.5	3.4	7.1		
Agrostis spp.	58.1		12.5	15.5	4.3		
Caltha phylloptera	58.1	16.1	31.3	12.1	2.5		
Carpha rodwayii	35.5	93.5	37.5		1.4	6.7	
Erythranthera australis	16.1	96.8		1.7			
Centrolepis monogyna	6.5	54.8		5.2	4.3	15.6	
Ewartia planchonii	9.7	29.0	50.0	12.1	7.1	2.2	
Carex hypandra		100.0			1.4		
Liverworts		41.9					
Dislaspis cordifolia	19.4	12.9	37.5	19.0	2.9		2.9
Oreomyrrhis ciliata	9.7	16.8	31.3	24.1	4.3	11.1	
Carpha alpina		74.2	37.5	14.0	1.4	8.9	8.8
Acaena montana	6.5		25.0	25.8	2.9		
Mosses	35.5	96.8	93.8	89.7	38.6	31.1	67.6
Gnaphalium traversii	6.5		100.0	55.2	20.0		5.9
Drosera arcturi		100.0	100.0			100.0	
Oreobolus pumilio		83.9	37.5	12.1		68.9	20.6
Gentianella diemensis		51.6	31.3	20.7		17.8	11.8
Poa gunnii	3.2	6.5	56.3	39.7	48.6	6.7	44.1
Mitrasacme archeri		41.9	31.3	1.7	1.4	73.3	23.5
Abrotanella scapigera			62.5	69.0	14.3	6.7	5.9
Celmisia saxifraga		58.1	56.3	74.1	30.0	8.9	50.0
Danthonia spp.		9.7	81.3	77.6	20.0	33.3	58.8
Abrotanella forsteroides						22.2	
Schoenus calyptratus			62.5	100.0	1.4	20.0	100.0
Luzula sp.	3.2		56.3	29.3	32.1	2.2	35.3
Dracophyllum minimum			12.5			71.7	8.8
Richea sprengelioides			12.5	1.7	10.0	22.2	14.7
Astelia alpina		9.7		29.3	37.5	40.0	50.0
Helichrysum backhousii			12.5	29.3	44.3		17.6
Actinotus suffocata						24.4	23.5
Oreobolus acutifolius				26.1	1.4	4.4	29.4
Lichens					17.1	55.6	100.0
Celmisia longifolia		3.2	6.3	1.7	15.7	13.3	58.8
Erigeron stellatus			6.3	5.2	15.7	4.4	44.1
Cyathodes dealbata							20.6
Pentachondra pumila				1.7	7.1	6.7	64.7
Rubus gunnianus					8.6	11.1	32.4

* Only taxa with at least 20% frequency in one group shown.

relatively flat relief with deep finely textured soils, directly below the zone of maximum snow accumulation (Figs 1, 5, 6; Table 3). At the other extreme are the mat heath (group 2) and the shrub fjaeldmark (group 6) communities. These form on areas of steepest slope, have shallow, relatively coarse soils, and consequently are subject to rapid soil drainage and low soil water storage capacity (Figs 1, 5, 6; Table 3).

Axis 2 is correlated with the environmental gradients associated with variation in duration of snow cover. The bolster heaths (group 7) appear first and the fjaeldmark communities (groups 5 and 6) last. This pattern reflects the topography of the area (Figs 5, 6).

Our data also indicate that the short alpine herbfield and *Abrotanella forsteroides* bolster heath have a lesser duration of snow cover than *Dracophyllum minimum* bolster heath and the two mat heath communities; and that these communities in turn have a lesser duration of snow cover than the two fjaeldmark communities. Absolute figures for duration of snow cover could be meaningful only with many years records. However, past observations of the snow patch strongly suggest that the pattern of disappearance of snow is constant between years.

The topographic positions occupied by the various vegetation types (Figs 1, 5), their relationship to snow melt patterns, soil type (Table 3) and field observations have indicated that the short alpine

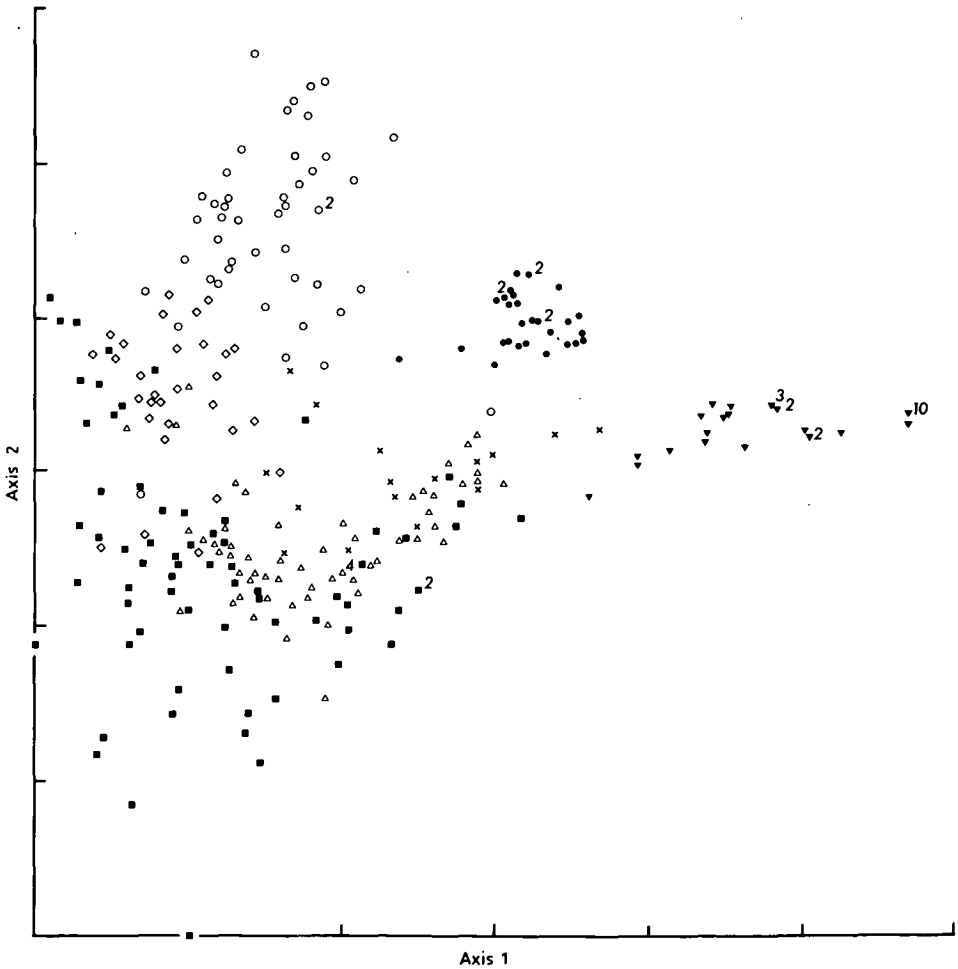

FIG. 4. Ordination of quadrat data using detrended correspondence analysis showing classificatory groups. 1(●) short alpine herbfield; 2(◊) matheath; 3(▼) short alpine herbfield; 4(×) short alpine herbfield/fjaeldmark transition; 5(△) herb fjaeldmark; 6(■) shrub fjaeldmark and 7(○) bolster heath. Figures indicate the number of quadrats at that point.

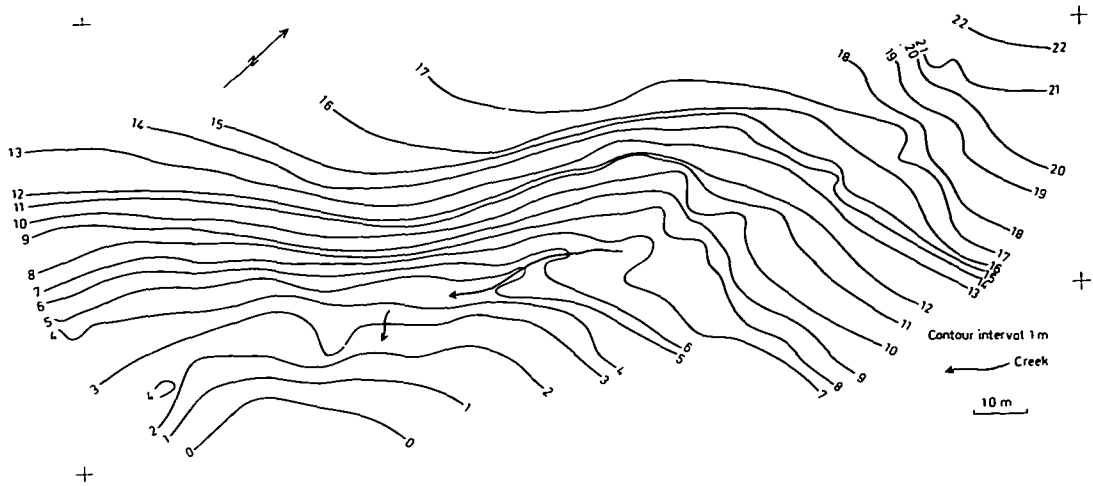

FIG. 5. Topographic map of snowpatch at Mt Field, Tasmania. Contour interval 1 m. Major drainage lines are shown.

herbfield is constantly moist with a development of sheet flow over a large part of its area at times of snow melt or heavy rainfall. Dry conditions are progressively more frequent in *Abrotanella forsteroides* bolster heath, *Dracophyllum minimum* bolster heath, herb fjaeldmark, shrub fjaeldmark and mat heath areas.

Nonsorted stone steps (Washburn 1979) have developed in the fjaeldmark. The risers are vegetated while the relatively flat treads are largely bare. The shrub fjaeldmark has more bare ground (Table 1), larger stone steps and a markedly higher percentage of gravel in its soil than the herb fjaeldmark (Table 3). In contrast the fans, occupied by the short alpine herbfield, have soils lacking gravel and consisting largely of the finer-sized particles. This leads to their having a larger capacity for storage of soil water. These soils are darker and less acid than those of the fjaeldmark (Table 3).

The relative abundance of wallaby scats (Table 1) is partly a function of the locations of appropriate topograhic traps for these ellipsoid objects. How-

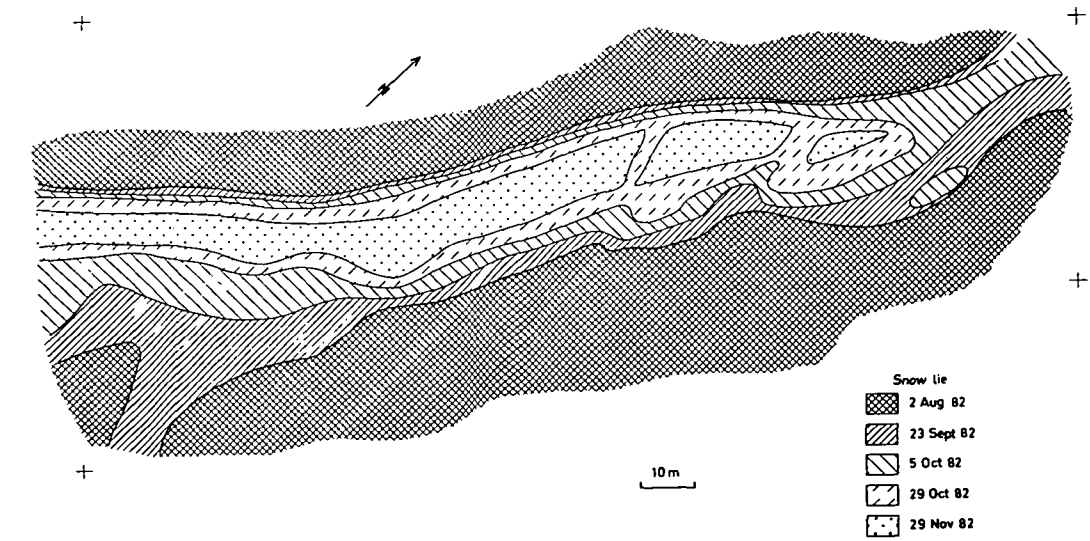

FIG. 6. Snow lie map of snowpatch at Mt Field, Tasmania. Position of snow boundary is indicated by date.

TABLE 3. Soil characteristics for the fjaeldmark and short alpine herbland

Site	Shrub fjaeldmark		Herb fjaeldmark		Short alpine herbfield Base of lobe
Depth (cm)	0–5 cm	5–10 cm	0–5 cm	5–10 cm	0–5 cm
(%)					
Gravel (> 2 mm)	94.60	78.77	42.69	14.96	–
Coarse sand (2 mm–63 μm)	5.40	19.56	40.52	53.94	52.52
Fine sand (63–20 μm)	–	0.64	10.47	17.67	21.85
Silt (20–2 μm)	–	0.64	5.78	8.01	14.84
Clay (< 2 μm)	–	0.39	0.54	5.42	10.79
pH	4.0	4.0	4.0	4.0	5
Colour*	2.5 Y 7/3 Light yellow	2.5 Y 5/3 Yellowish brown	10 YR 5/6 Yellowish brown	10 YR 5/8 Yellowish brown	10 YR 3/4 Dark brown

*Colour determined from Munsell Soil Colour Charts.

ever, their distribution implies that grazing activity is concentrated in the short alpine herbfield, the vegetation type richest in forbs and graminoids (Table 1).

Discussion

One of the most interesting features of the snow patch described above is the fjaeldmark associated with the area of longest snow lie. Comparable areas at similar altitudes on the dolerite of Mt Field develop *Astelia* herbland, indicating that there is a greater propensity towards fjaeldmark formation on the sedimentary rocks than on dolerite. In similar topographic situations on mudstone and sandstone elsewhere in Tasmania, fjaeldmark has not been observed to develop in this way, being confined to windward slopes and hill tops rather than leeward concavities (Kirkpatrick & Harwood 1980; Kirkpatrick 1984). However, the snow patch at Mt Field West is at a higher altitude than the Boomerang, Rocky Hill and Pyramid Mountain snow patches. Sparse vegetation cover and rocky, but not stepped, ground is typical of the higher altitude snow patches found on quartzite, as at Mt Campbell, Cradle Plateau and Frenchmans Cap. Areas of extended snow lie at Kosciusko tend to be rocky, with the interstices being vegetated by fjaeldmark dominated by *Coprosma* sp. and *Colobanthus nivicola* (Costin *et al.* 1979).

The bare ground in the fjaeldmark probably is not due to an inadequate growing season, as snow rarely persists for as long as at Kosciusko and the risers are vegetated. However, occasional successive years of longer than normal snow persistence may create bare ground which would tend to maintain itself on these highly fissile Permian sediments, because year-round needle ice, frost-heaving and water erosion inhibit revegetation, particularly on the treads of the nonsorted stone steps. Where the treads have been invaded, it has been by moss and rhizomatous rosette species such as *Celmisia saxifraga, Abrotanella scapigera* and *Senecio pectinatus*.

The hypothesis that more severe conditions have existed in the recent past is supported firstly, by the complete vegetation cover on some of the treads of the nonsorted steps in the less steep parts of the herb fjaeldmark, by the apparently recent invasion of the upper parts of the most northerly patch of short alpine herbfield by the bolster plant *Abrotanella forsteroides*, and lastly, by a similar apparent invasion of the lower parts of the herb fjaeldmark by another bolster species, *Dracophyllum minimum*.

Short alpine herbfields are typical of areas receiving irrigation from snow patches both in Australia and elsewhere (Costin 1954). The enrichment of the short alpine herbfield by fine mineral particles deposited on snow or eroded from beneath snow is also typical, substantially increasing its soil water holding capacity (Costin *et al.* 1979). At Mt Field the short alpine herbfields do not form extensive peats, unlike their counterparts at Kosciusko (Costin *et al.* 1979).

The vascular plant flora associated with snow-patches at Kosciusko has been reasonably well documented by McVean (1969) in his *Celmisia longifolia, Plantago muelleri-Conostomum cur-*

virostre and *Coprosma pumila* associations and by Costin *et al.* (1979) in their short alpine herbfield. In total these authors list 71 species in 46 genera. We observed 67 vascular plant species from 51 genera from the environments associated with one small snow patch on one mountain. Eleven species occur in both areas: *Carex hypandra, Erythranthera australis, Oreobolus pumilio, Schoenus calyptratus, Scirpus subtilissimus, Juncus antarcticus, Celmisia longifolia, Drosera arcturi, Erigeron stellatus, Pentachondra pumila* and *Senecio pectinatus*. This list could be extended if other Tasmanian snow patches were considered. There are also many cases of vicarious species such as *Caltha introloba, C. phylloptera, Diplaspis hydrocotyle* and *D. cordifolia*. In fact, at the generic level there is a high degree of similarity between the two snow patch floras, 18 genera being shared.

Acknowledgments

We would like to thank the staff of the Tasmanian Herbarium for help in identification, two helpful referees, Dr G. van de Geer for drawing the figures, Denis Charlesworth for the soil analyses and Terese Hughes for typing the manuscript.

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(Final manuscript received October 1984)

REGENERATION CHARACTERISTICS OF A SWAMP FOREST IN NORTHWESTERN TASMANIA

by N. Gibson, K. Williams, J. Marsden-Smedley and M.J. Brown

(with one table and five text-figures)

GIBSON, N., WILLIAMS, K., MARSDEN-SMEDLEY, J. & BROWN, M.J., 1987 (30:vi): Regeneration characteristics of a swamp forest in northwestern Tasmania. *Pap. Proc. R. Soc. Tasm.*, 121: 93-100. ISSN 0080-4703. National Parks and Wildlife Service, P.O. Box 210, Sandy Bay, Tasmania 7005; and Forestry Commission, 199 Macquarie Street, Hobart, Tasmania 7000 (MJB).

The botanical composition and regeneration characteristics are described for a *Melaleuca ericifolia-Leptospermum lanigerum* forest from northwestern Tasmania. The size classes of the two dominant species are highly correlated with tree age. Size class analysis shows that the dominants are regenerating continuously. The relationship of this forest type to rainforest and wet sclerophyll forest are discussed.
Key Words: Tasmania, swamp forest, regeneration, *Melaleuca, Leptospermum*

INTRODUCTION

The forests of Tasmania traditionally are treated at the formation level as either sclerophyll forest or as rainforest (e.g. Jackson 1965, Curtis 1965-66, Gilbert 1970-71). The sclerophyll forests are broken into two classes, wet and dry sclerophyll, each of which has a characteristic understorey flora. The dry sclerophyll forests are dominated by either *Eucalyptus* or *Casuarina* (Duncan & Brown 1985), whilst wet sclerophyll forests are *Eucalyptus*-dominated. The dominant species of the two subformations have quite different regeneration modes, with dry sclerophyll dominants being either continuous or pulse regenerators while most wet sclerophyll forests are either even-aged or contain only a few age-classes, depending on the past history of fires.

Jarman & Brown (1983) have defined cool temperate rainforest in Tasmania as those forest communities dominated by species of *Nothofagus*, *Atherosperma*, *Eucryphia*, *Athrotaxis*, *Lagarostrobos*, *Phyllocladus* or *Diselma* of at least 8 m in height. Rainforest species are defined as those species able to perpetuate themselves (either vegetatively or from seed) within forests dominated by one or more of the species listed above.

In northwestern Tasmania there are large tracts of closed swamp forest which are usually dominated by *Acacia melanoxylon* or *Melaleuca ericifolia* (Kirkpatrick & Dickinson 1984, fig. 1). These forests subsume a range of community types from almost pure *A. melanoxylon* forests through *A. melanoxylon*-Myrtaceae-*Nothofagus*(-*Phyllocladus*) dominated forests to almost pure *Leptospermum* and/or *Melaleuca* forest (Anon. 1982, Jarman & Brown 1983, Jarman *et al.* 1984, R. Mesibov *pers. comm.* 1986).

Jarman & Brown (1983) considered that whilst *Leptospermum lanigerum*, *L. nitidum*, *L. scoparium* and *Melaleuca squarrosa* may be found in the rainforest canopy, they were doubtful rainforest species, and suggested that detailed studies were required to determine their status. Thus Jarman *et al.* (1984) point out that the niche occupied in rainforest by these myrtaceous species may be that of a "good" rainforest species or may instead be similar to that filled by *Eucalyptus* in the mixed forests of Gilbert (1959).

The relationships of the swamp forests to either rainforests or to sclerophyll forests have not been determined. The floristic variation they contain apparently ranges from predominantly rainforest elements to predominantly sclerophyllous and the regeneration characteristics of the non-eucalypt dominants have not been described. The aim of the present paper is to provide a floristic description of one such swamp forest and to investigate the regeneration strategies of the two forest dominants — *Leptospermum lanigerum* and *Melaleuca ericifolia*.

THE STUDY AREA

The study area is located on the Welcome River in the far northwest of the State. This area lies in the warm-humid climatic zone (Gentilli 1972) with a winter rainfall maximum. The swamp

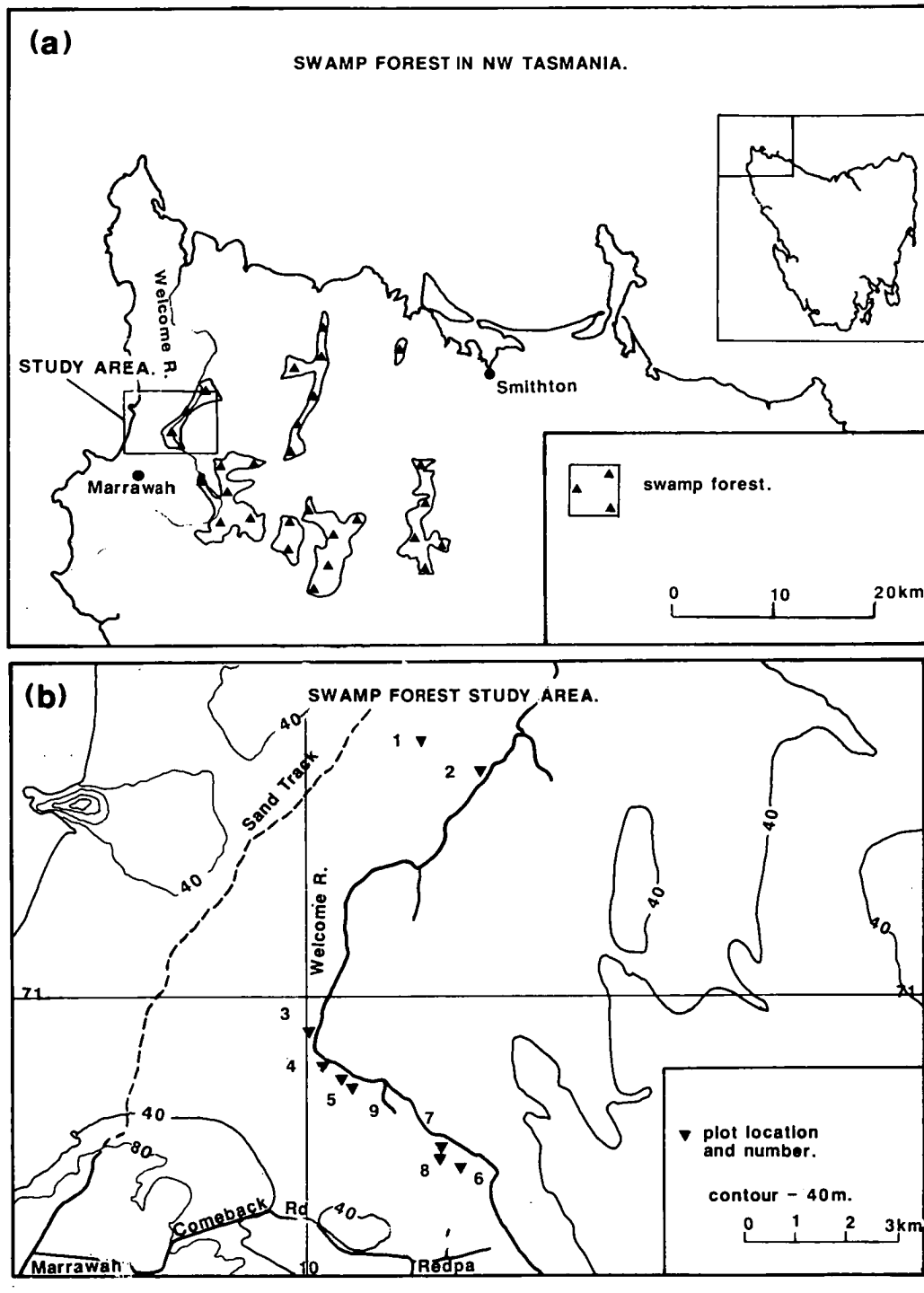

FIG.1 — (a) The occurrence of swamp forest in northwestern Tasmania (after Kirkpatrick & Dickinson 1984), and (b) the location of the study area.

forests of this area are commonly inundated in the winter months.

The topography is of a broad flat valley, the vegetation being underlain by Holocene alluvium, sand and gravel. The swamp forest in the area is dominated by *Melaleuca ericifolia* with *Leptospermum lanigerum* also being present.

METHODS

Vegetation data were collected from nine plots along the Welcome River between Redpa and Boggy Creek. Both structural and floristic data were recorded from 20 m diameter plots using the TASFORHAB system of Peters (1984). From these data a vegetation description was compiled and a generalized vegetation profile was constructed.

In the area presently being cleared to make drainage channels, 49 basal slabs of *Melaleuca ericifolia* from 10 to 460 mm diameter were collected for ageing of the trees. Nine slabs of *Leptospermum lanigerum* from 10 to 600 mm diameter were also collected. Slab diameters were determined with a diameter tape and ring counts were made on their planed tops. From these data a simple linear regression was made between age and size. Size-class analyses were undertaken from six sites. At each site, a 10 × 10 m plot was established and all individuals greater than 100 mm diameter were counted and diameters at breast height (DBH) recorded. A 5 × 5 m subplot was located in one corner of the plot and all individuals less than 100 mm diameter were counted. Size class histograms were constructed from these data.

The size distributions were then modelled against the power function $y = y_o x^{-b}$ and the negative exponential $y = y_o e^{-bx}$, where y is the number of individuals in size class x, y_o is the initial population size and b is mortality. The power function is appropriate to forest stands in which there is continuous regeneration with a mortality that decreases with increasing age, whilst the negative exponential reflects constant mortality (Hett & Loucks 1976). These models were tested for the four plots of *Melaleuca ericifolia* for which data were available in at least five size classes.

As a further check on the regeneration mode of the two species, increment counts were made from rings near the centre and at the outside of stem slabs. These measurements were made to determine whether there was any indication that episodic release from suppression of more or less even-aged stems was giving rise to apparent continual regeneration.

Nomenclature follows Curtis (1963, 1967), Curtis & Morris (1975), Willis (1970), and Jones & Clemesha (1981).

RESULTS

Vegetation

The vegetation of the area is dominated by a closed canopy of *Melaleuca ericifolia* with *Acacia melanoxylon* and *Leptospermum lanigerum* as sub-dominants. The canopy also contains occasional individual trees of *Eucalyptus ovata* and *E. obliqua* on better-drained sites. The understorey is dominated by *Melaleuca ericifolia* with *Coprosma quadrifida*, *Drimys lanceolata*, *Leptospermum lanigerum* and occasionally *Pomaderris apetala*, again on better drained sites. The ground layer contains *Gahnia grandis* and *Lepidosperma elatius* together with the ferns *Polystichum proliferum*, *Blechnum nudum* and *Dicksonia antarctica*. Epiphytic ferns, including *Microsorium diversifolium*, *Hymenophyllum peltatum*, *Ctenopteris heterophylla* and *Grammitis billardieri* were occasionally present. A generalized vegetation profile is shown in figure 2. At the time of sampling (June) the free water surface was at or above ground level in most of the area traversed.

Regeneration Modes of the Dominant Species

A highly significant correlation was found between diameter and age for both *Melaleuca ericifolia* and *Leptospermum lanigerum* (figs 3 and 4). Thus size of stem provides a reasonable means of estimating age. Examination of the incremental growth of individual stems indicated that considerable suppression of individuals was occurring through the stand, but there was no indication that the initial regeneration resulted from a single disturbance event, nor that the release of individuals was tied to some broad scale disturbance such as fire or windthrow. Thus size class analysis can be used to describe adequately the population dynamics of those samples for which data are available. In all of the plots, there were large numbers of seedlings and saplings (individuals less than 100 mm diameter) found under closed canopies (fig. 5). In plots 1, 2, 3 and 5, size class distributions fitted the power function model (table 1).

DISCUSSION

The occurrence of large numbers of seedlings and saplings scattered through the forest suggests

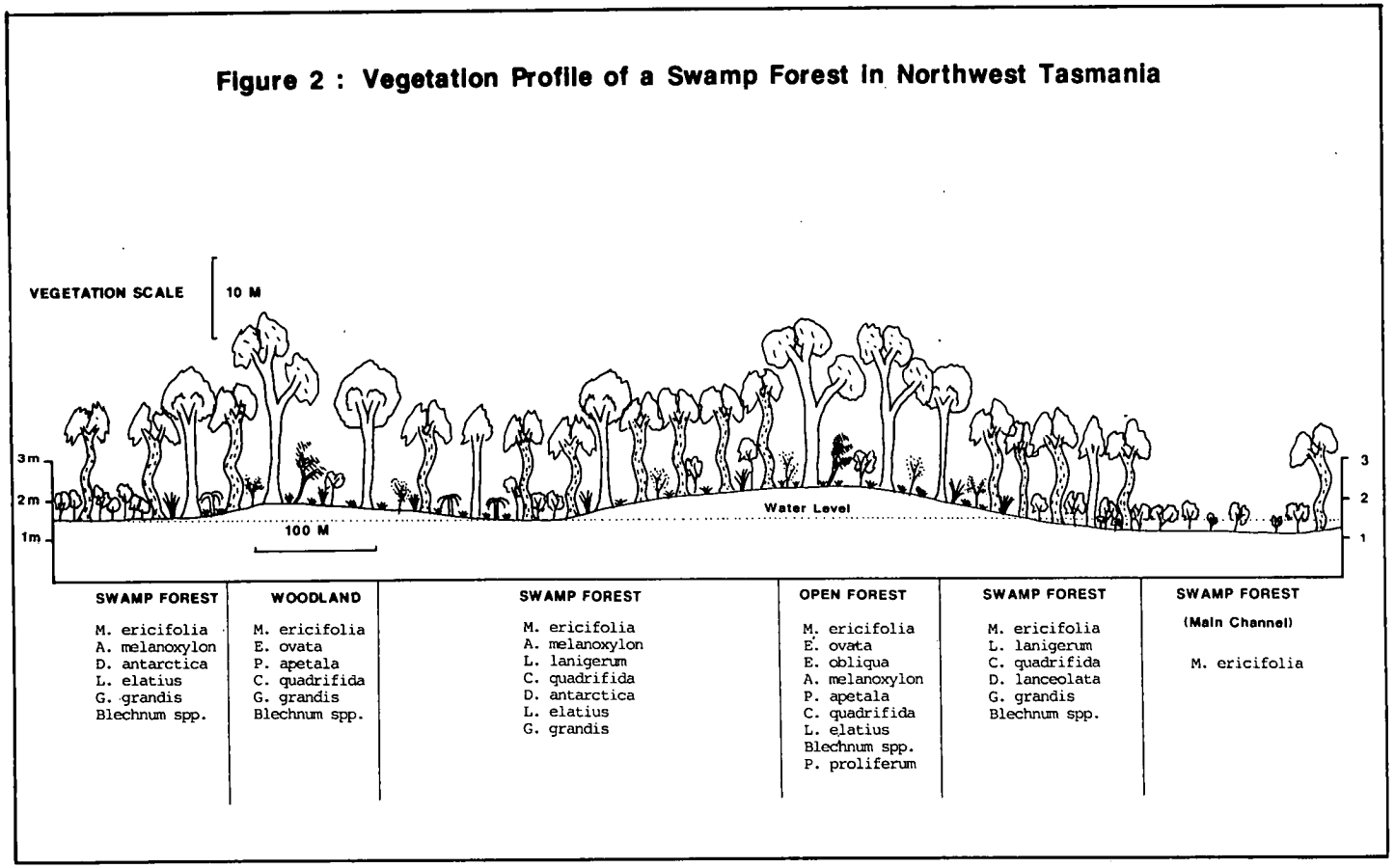

FIG.2 — Vegetation profile of a swamp forest in northwestern Tasmania.

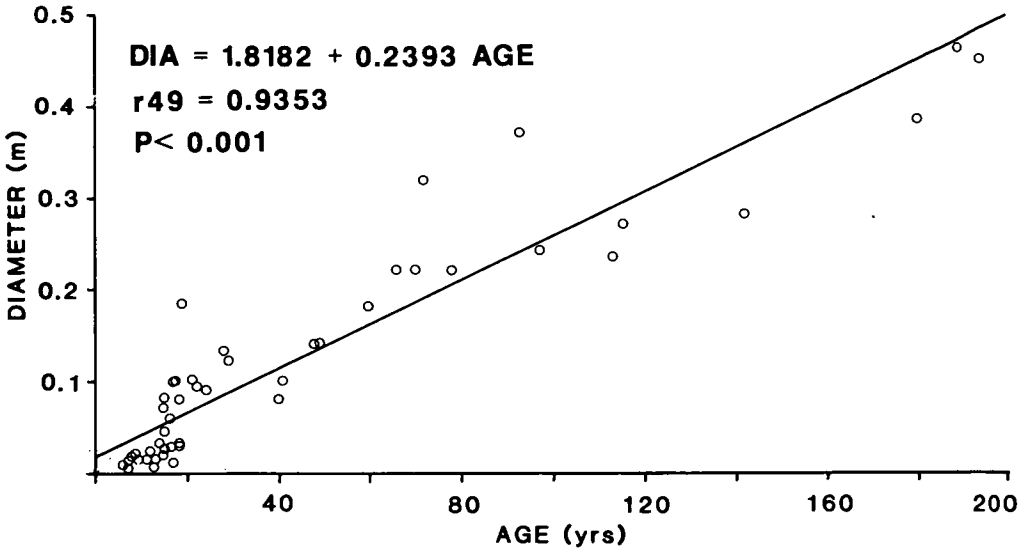

FIG.3 — Regression of diameter on age for Melaleuca ericifolia.

that *Melaleuca ericifolia* is capable of continuous regeneration in an essentially closed-canopy forest. This observation is confirmed by the age and size class analyses and the fit to the power function. However, although there is a highly significant correlation of size and age, it is apparent from the increment counts that growth rates are variable and that suppression can occur for periods in excess of 20 years. Further analyses of the pattern

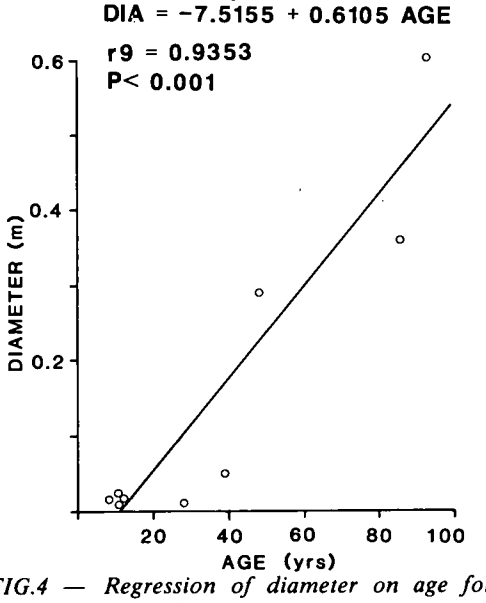

FIG.4 — Regression of diameter on age for Leptospermum lanigerum.

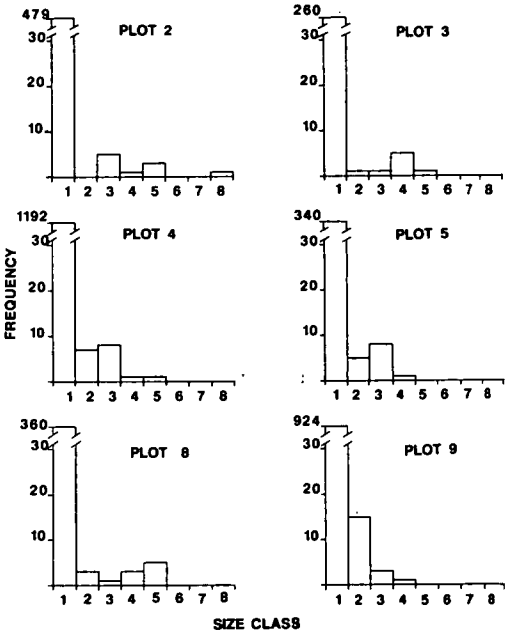

FIG.5 — Frequency-size class distributions for Melaleuca ericifolia *from six sample plots. Stems grouped into 100 mm size classes.*

TABLE 1

Size class (x) and frequency (y) relationships for four samples taken within the *Melaleuca ericifolia* swamp forest. (a) Exponential function, (b) Power function.

Sample no.	Relationship	r	P
1	(a) $\ln(y+1) = 38.411-0.513x$	-0.608	
	(b) $\ln(y+1) = 20.796-1.277\ln x$	-0.633	<0.05
2	(a) $\ln(y+1) = 88.269-0.864x$	-0.648	
	(b) $\ln(y+1) = 67.997-2.347\ln x$	-0.762	<0.05
3	(a) $\ln(y+1) = 897.823-1.417x$	-0.850	<0.05
	(b) $\ln(y+1) = 488.947-3.720\ln x$	-0.920	<0.01
4	(a) $\ln(y+1) = 111.756-0.848x-$	0.634	
	(b) $\ln(y+1) = 108.400-2.566\ln x$	-0.783	<0.05

of occurrence of seedlings in relation to tree death and canopy gaps would be necessary to determine absolutely whether the observed release from suppression is light (cf. Duncan 1981, Ogden 1985, Read & Hill 1985) or moisture-related (cf. Bowman & Kirkpatrick 1986). However, regenerating seedlings and saplings of *Leptospermum lanigerum* were always present in higher numbers than *Melaleuca ericifolia* under canopy gaps and adjacent to forest edges.

The goodness-of-fit to the power function model suggests that highest mortality occurs in the smaller size classes, but once stems are larger than about 100-200 mm DBH, there is a high probability that they will grow through to old age (i.e. in excess of 200 years). Less data are available for *Leptospermum lanigerum*, but it also appears to have a linear size-age relationship.

The oldest trees in this forest are approximately 200 years old. The age to senescence of *Melaleuca ericifolia* (and of *Leptospermum lanigerum*) is unknown but species of both *Melaleuca* and *Leptospermum* are found as codominants in rainforests (e.g. Jarman & Crowden 1978, Jarman *et al.* 1984), some of which are known to be at least 300 years old (e.g. Brown & Podger 1982). Elsewhere in the northwestern region, these species occur in swamp forests together with *Nothofagus*, *Phyllocladus* and such rainforest understorey shrub species as *Trochocarpa cunninghamii* and *Anopterus glandulosus* (Anon. 1982), and the whole of the region is climatically suited to the growth of rainforest (Jackson 1965).

Thus there may be a seral and/or successional relationship in which these relatively young Myrtaceae-dominated forests are eventually replaced by forests containing the more usual rainforest dominants. However there is no evidence in the present case of colonization by any rainforest species *sensu* Jarman & Brown (1983) (see appendix). An alternative interpretation is that the *Melaleuca* (and/or *Acacia melanoxylon*) swamp forests represent a deflected climax vegetation, whose occurrence is related to the poor drainage and longevity of seasonal inundation. Further work is necessary to determine whether *Melaleuca/Leptospermum* are able to grow in periodically anoxic conditions which may limit the growth of *Nothofagus* and *Phyllocladus*. Until such work is undertaken, it is not possible to determine whether *Melaleuca ericifolia* or *Leptospermum lanigerum* in these swamp forests are behaving as "good" rainforest species (cf. Jarman *et al.* 1984).

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(accepted 17 March 1987)

APPENDIX

Check-list of vascular plants found in the *Melaleuca ericifolia* swampforest.

PTERIDOPHYTA

Aspidiaceae
Polystichum proliferum

Blechnaceae
Blechnum nudum
Blechnum wattsii

Dennstaedtiaceae
Histiopteris incisa
Hypolepis rugosula

Dicksoniaceae
Dicksonia antarctica

Grammitidaceae
Ctenopteris heterophylla
Grammitis billardieri

Hymenophyllaceae
Hymenophyllum peltatum
Hymenophyllum sp.

Polypodiaceae
Microsorium diversifolium

ANGIOSPERMAE: DICOTYLEDONEAE

Apiaceae
Hydrocotyle javanica

Apocynaceae
Parsonsia straminea

Asteraceae
Cirsium sp.
Helichrysum dendroideum
Senecio sp.

Brassicaceae
Brassica sp.
Cardamine heterophylla

Elaeocarpaceae
Aristotelia peduncularis

Mimosaceae
Acacia melanoxylon

Myrtaceae
Eucalyptus obliqua
E. ovata
Leptospermum lanigerum
Melaleuca ericifolia
M. squarrosa

Onagraceae
Epilobium hirtigerum

Oxalidaceae
Oxalis corniculata

Pittosporaceae
Billardiera longiflora

Polygonaceae
Muehlenbeckia gunnii

Ranunculaceae
Clematis aristata
Ranunculus sp.

Rhamnaceae
Pomaderris apetala

Rosaceae
Acaena novae-zelandiae

Rubiaceae
Coprosma quadrifida

Thymelaeaceae
Pimelea drupacea

Winteraceae
Drimys lanceolata

ANGIOSPERMAE: MONOCOTYLEDONEAE

Cyperaceae
Carex appressa
Gahnia grandis
Lepidosperma elatius
Schoenus maschalinus
Scirpus fluitans

Juncaceae
Juncus effusus

A FOSSIL BOLSTER PLANT FROM THE KING RIVER, TASMANIA

by N. Gibson, K.W. Kiernan and M.K. Macphail

(with two tables, two text-figures and three plates)

GIBSON, N., KIERNAN. K.W. & MACPHAIL, M.K., 1987 (30:vi): A fossil bolster plant from the King River, Tasmania. *Pap. Proc. R. Soc. Tasm.*, 121: 35-42. ISSN 0080-4703. Departments of Geography and Botany (N.G.), Department of Geography (K.W.K.) and Department of Botany (M.K.M.), University of Tasmania, Hobart, Tasmania.

A macrofossil of the alpine bolster plant *Donatia novae-zelandiae* was found in the King River Valley, approximately 230 m above sea level in central western Tasmania. The fossil was in situ on a palaeosol that appears to have formed immediately prior to the late Last Glacial Maximum. An age of 21 180 + 370 years b.p. was established by radiocarbon dating. Pollen and present day distributional data suggest that the tree line was then at least 750 m lower than at present, implying a temperature depression of about 4.5° C. Scanning electron-micrographs and photomicrographs of the extant and fossil bolster species are presented.

Key Words: Tasmania, bolster, *Donatia*, fossil, palaeosol.

INTRODUCTION

Bolster plants are chamaephytes with a very compact growth habit, the branches being closely packed, with short internodes forming a hard hemispherical surface. This growth form is common in alpine areas of Tasmania, New Zealand, South America and some of the sub-Antarctic Islands (Godley 1978). The bolster form is poorly developed in the alpine areas of mainland Australia. The term bolster is preferred to cushion to indicate the hard compact nature of this growth form compared with Northern Hemisphere species of cushion plants.

In Tasmania there are four major species of bolster plant, *Abrotanella forsteroides* (Hook.f.) Benth. (Asteraceae), *Dracophyllum minimum* (Epacridaceae), *Phyllachne colensoi* (Stylideaceae) and *Donatia novae-zelandiae* (Donatiaceae). These species are initially difficult to distinguish in the field in the vegetative phase. They can form hard cushions up to 3.0 m diameter and 0.5 m tall. Distribution patterns found in these species have been described by Martin (1950), Jackson (1972), Kirkpatrick (1977, 1980, 1982, 1983) and Kirkpatrick & Harwood (1980), Brown *et al.* (1983), Kirkpatrick & Gibson (1984) and Gibson & Kirkpatrick (1985a,b).

The difficulty of ascribing the terms alpine and subalpine to the high altitude treeless areas of Tasmania, where treelines are generally absent, has been discussed by Kirkpatrick (1982). Notwithstanding this, bolster plant distribution in Tasmania is generally described as alpine with incursions below the climatic treeline in areas subject to cold air drainage and poor soil drainage. This paper records a macrofossil of the cushion plant *Donatia novae-zelandiae* from the King River Valley approximately 750 m below the present climatic treeline in central western Tasmania, and discusses its stratigraphic context and its significance in relation to present day distributional patterns.

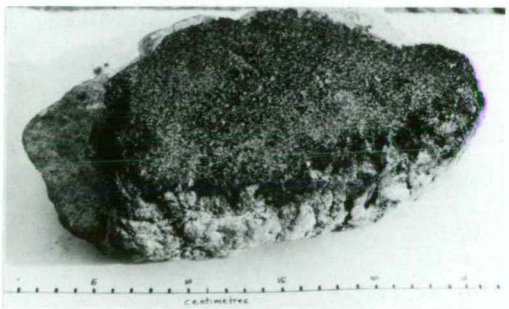

PLATE 1 — Photograph of a fossil Donatia novae-zelandiae *cushion (21 180 years b.p.) from the Dante Rivulet site.*

METHODS

The 200 mm diameter fossil was collected during an investigation of the glacial chronology of the central West Coast Range. It was obtained from a 5 m deep section cut by the King River a

short distance downstream from its confluence with the Dante Rivulet at about 230 m ASL (plate 1, figs 1 and 2). By this means it was possible to relate the fossil *Donatia* to the regional lithostratigraphy and chronostratigraphy. The immediate area has been subject to repeated firing, the present vegetation consisting of heathy sedgeland with riparian strips of mixed forest.

Positive identification of the fossil was carried out using both cuticular analysis and scanning electron microscopy of the leaf surface. Leaf fragments were initially soaked in hydrofluoric acid for 24 hours to remove siliceous material. The most intact fragments were mounted for scanning electron microscopy. The remaining material was cleared with nitric acid, and the cuticles prepared by soaking in nitric acid and potassium chlorate neutralising with aqueous ammonia and finally staining with safranin O and mounting. Comparative slides of all four extant bolster species were similarly prepared.

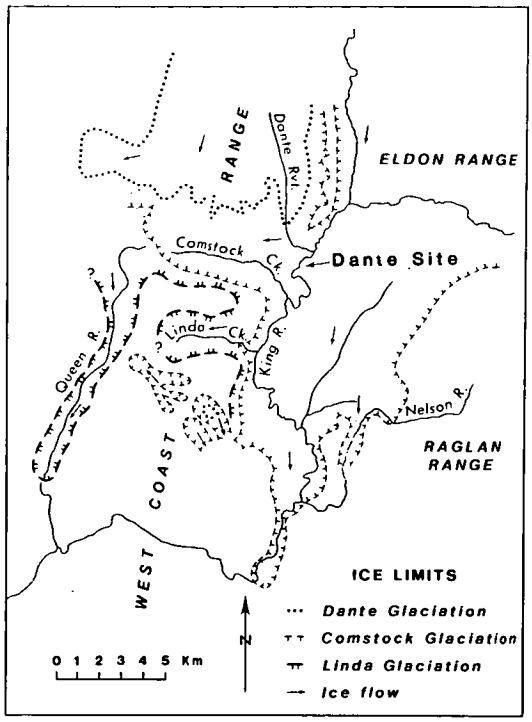

FIG. 1 — Topographic relationships and Quaternary ice limits near the Dante Rivulet site in the central West Coast Range (after Kiernan, 1983a).

A spot pollen sample was taken from the organic silts at the downstream end of the palaeosol. Pollen and spore types were extracted using standard palynological techniques (Faegri & Iverson 1975).

Species nomenclature follows Curtis (1963, 1967) and Curtis & Morris (1975), unless otherwise stated.

RESULTS

Stratigraphy

The exposed profile is shown in figure 2. The lowermost metre of the section consists of coarse gravels and gritty sand that probably represent part of the Comstock Formation but could be more recent. It is believed to represent glacial outwash derived from an ice body which lay a short distance upstream in the King Valley. This unit is unconformably overlain by 0.15 m of very dark brown (7.5 YR2/3) organic silt at the base of which abundant macrofossils were found including small branchlets which are believed to have been river transported. The spot pollen sample taken from this unit indicates an Asteraceae-Poaceae assemblage (table 1).

A weakly developed podsolic palaeosol occurs upon this silt unit. The intact cushion macrofossil was about 0.2 m in diameter and was found *in situ* on the palaeosol. The palaeosol is in turn overlain by 0.45 m of slightly discoloured yellowish grey (2.5 Y5/1) silt and fine sands which were probably rapidly deposited in an aquatic environment. The cushion plant itself has been radiocarbon dated at 21 180 ± 370 years b.p. (SUA2154). A 0.2 m piece of driftwood was recovered from 0.1 m above the palaeosol and dated at 18 800 ± 500 years b.p. (ANU2533). A further date of 20 100 ± 470 years B.P. (SUA2155) has been obtained from twigs incorporated in a silt bed that overlies the Comstock gravels about 100 m downstream from the fossil cushion. This silt is believed to be equivalent to that immediately beneath the cushion plant, but exposure is discontinuous and this relationship remains unproven (Kiernan 1980, 1985).

A further 0.35 m of yellowish grey (2.5 Y6/1) fine sand and silt is succeeded by three metres of gravels of the Dante Formation which are interpreted as glacial outwash from a new ice advance in the tributary Dante Rivulet. The section is overlain by a metre of peat (Kiernan 1980, 1983a).

Pollen Analysis

Table 1 lists pollen and spore types extracted from the organic silt. Included against each taxon

TABLE 1

Spot pollen sample from Dante palaeosol and an estimate of pollen production/dispersal characteristics.

NI = no information, SU = severely under-represented, U = under-represented, W = well to over-represented.

Pollen Taxon	Percentage	Pollen Dispersal
Isoetes	+	NI
Lycopodium deuterodensum	+	U
L. scariosum	1.0	W
Gleichenia	14.0	U
Microstrobos	+	NI
Casuarina type	2.0	W
Chenopodiaceae	2.0	W
Compositae	20.0(3.0)	W
Donatia	2.0	SU
Epacridaceae T-type	9.0	SU
Leucopogon type	+	U
Monotoca	+	NI
Nothofagus fusca type	+	W
Eucalyptus	2.0	W
Melaleuca	+	W
Papilionaceae	+U	
Bellendena	+	NI
Orites	+	U
Coprosma	+	W
Rutaceae cf. *Phebalium*	+	NI
Cyperaceae	9.0	W
Drosera arcturi	+	NI
Gentianaceae cf. *Centaurium*	+	NI
Gentianella	+	NI
Goodeniaceae	+	W
Gramineae	17.0	W
Gunnera	+	SU
Astelia	+	NI
Lobeliaceae cf. *Lobelia*	+	NI
Plantago	+	U
Anemone	+	NI
Ranunculus	+	SU
Restionaceae	4.0	U
Scrophulariaceae cf.	+	NI
Umbelliferae Indet.	8.0	SU
Pollen sum:	64.8	

() refers to short echinate type probably extinct.

is an estimate of the pollen production/dispersal characteristics (=representivity) of the source plant(s) (cf. Macphail & McQueen 1983). All percentags are expressed relative to a pollen sum comprising the well-dispersed types (Macphail 1975).

Although the concentration of palynomorphs was low, 35 pollen types could be identified to a family or genus. The majority of these are herbs and, assuming the sources of the composite pollen were largely herbaceous, then herbs and pteridophytes constitute 70% of the pollen sum: Compositae (20%), Gramineae (17%), *Gleichenia* (14%), Cyperaceae plus Restionaceae (13%) and Umbelli-

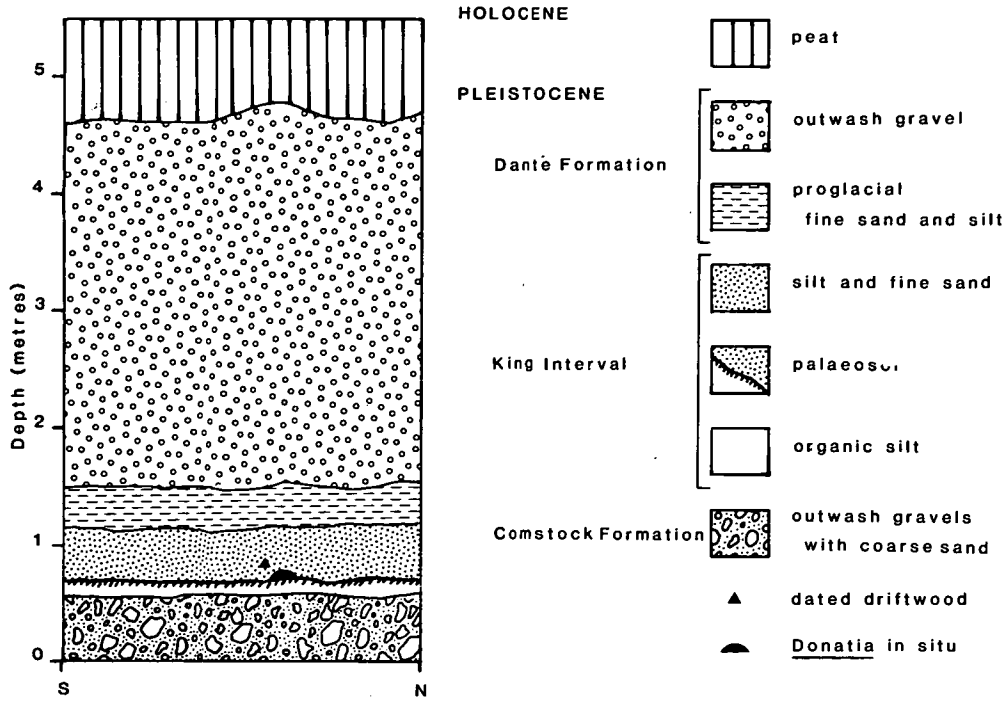

FIG.2 — Stratigraphy of section cut by the King River with locations.

ferae (8%). Woody types are comparatively infrequent with Epacridaceae (9%), *Eucalyptus*, *Casuarina* and *Donatia* (all 2%) being the most abundant. With the exception of *Microstrobos* and *Nothofagus gunnii* (*N. fusca* type), both of which have their main centres of distribution close to or above the timberline, pollen of rainforest taxa are absent. The 2% *Donatia* pollen is amongst the highest values of this type recorded to date in either fossil or modern assemblages in Tasmania (Macphail 1979, unpublished results, cf. fig. 3 in Colhoun 1985a).

Donatia Macrofossil

The photomicrographs of the cuticle and the electron micrographs of the leaf surface of the fossil are almost identical in detail with those of extant *Donatia novae-zelandiae* (plate 2), though somewhat smaller in size. Both show a distinctive raised cuticular ridge around the stomata. The leaf tips of both are bluntly acuminate. The typical dense tufts of axil hairs of *D. novae-zelandiae* are apparent in the cuticle preparations of the fossil.

Plate 3 (A to F) shows the distinctive patterns of surface cuticle, cell wall arrangement and gross stomatal size and pattern for the other three species of bolster plant. Electron micrographs of the leaf apices of these species also show distinctive differences.

Dracophyllum minimum is roughly triangular in cross-section near the leaf apex with each edge minutely serrate ending in an acute point. The stomata are very small, less than 15 μm long and epidermal cells have highly distinctive sinuous walls.

Phyllachne colensoi has an obtuse apex with a glandular pore just below it, on the abaxial surface (Curtis 1963). The cuticle is very thin and the electron micrograph shows evidence of localized collapse.

Abrotanella forsteroides has a distinctive acuminate often recurved hair-like apex with obscurely blunt serrulate leaf margins. Stomata are arranged in bands around the leaf converging toward the apex. The photomicrograph (plate 3F) of one of these bands shows the thickened walls of epidermal cells and the electron micrograph (plate 3E) shows imprints of stomata in cuticle from the closely appressed imbricate leaves.

DISCUSSION

The Comstock Glaciations are considered to predate the Last Glacial Stage on morphologic,

stratigraphic and weathering evidence at several sites in the central West Coast Range (table 2). The silts which unconformably overlie the Comstock gravels at this section have been only weakly modified by pedogenesis. The grey silt which overlies the palaeosol is interpreted as having been rapidly deposited in an aquatic environment. The upper silts represent renewed glacigenic sedimentation in a surface depression after a time break. The radiocarbon dates indicate that the Dante outwash gravels represent the late Last Glacial maximum (Kiernan 1980, 1983b).

Both the macrofossil and microfossil evidence suggest that a cold climate, species-rich herbfield bog mosaic occupied the site during the period represented by the organic silt. Rainforest was absent and sclerophyll trees rare within the region, with the latter possibly occurring in shrub form.

Although this interpretation is ecologically consistent with current reconstructions of full glacial climates in western Tasmania (Macphail 1975, Macphail & Colhoun 1985), caution is required for several reasons. Firstly, the pollen sample is an isolated one and possibly unrepresen-

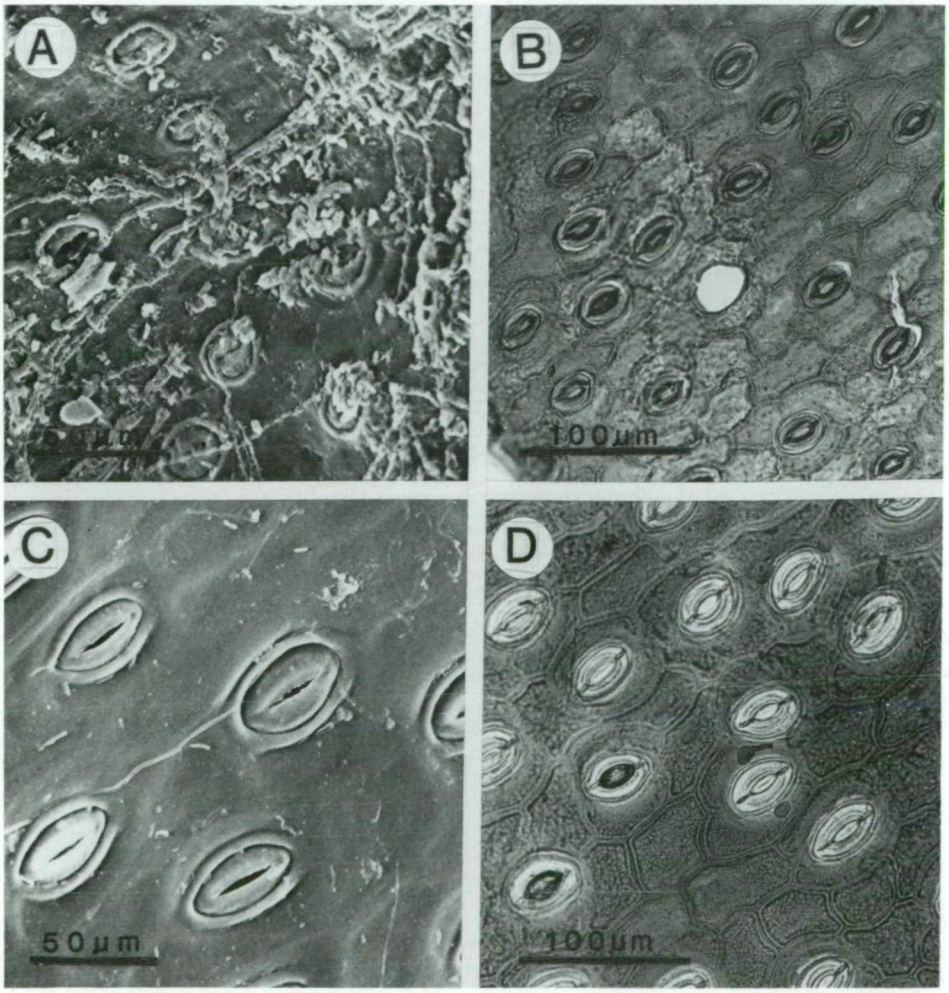

PLATE 2 — A, scanning electron micrograph of the fossil leaf surface; B, cuticular photomicrograph of the fossil showing guard cells and irregularly shaped epidermal cells; C, scanning electron micrograph of extant Donatia novae-zelandiae *leaf surface showing distinctive raised subsidiary cells; D, cuticular photomicrographs of extant* Donatia novae-zelandiae.

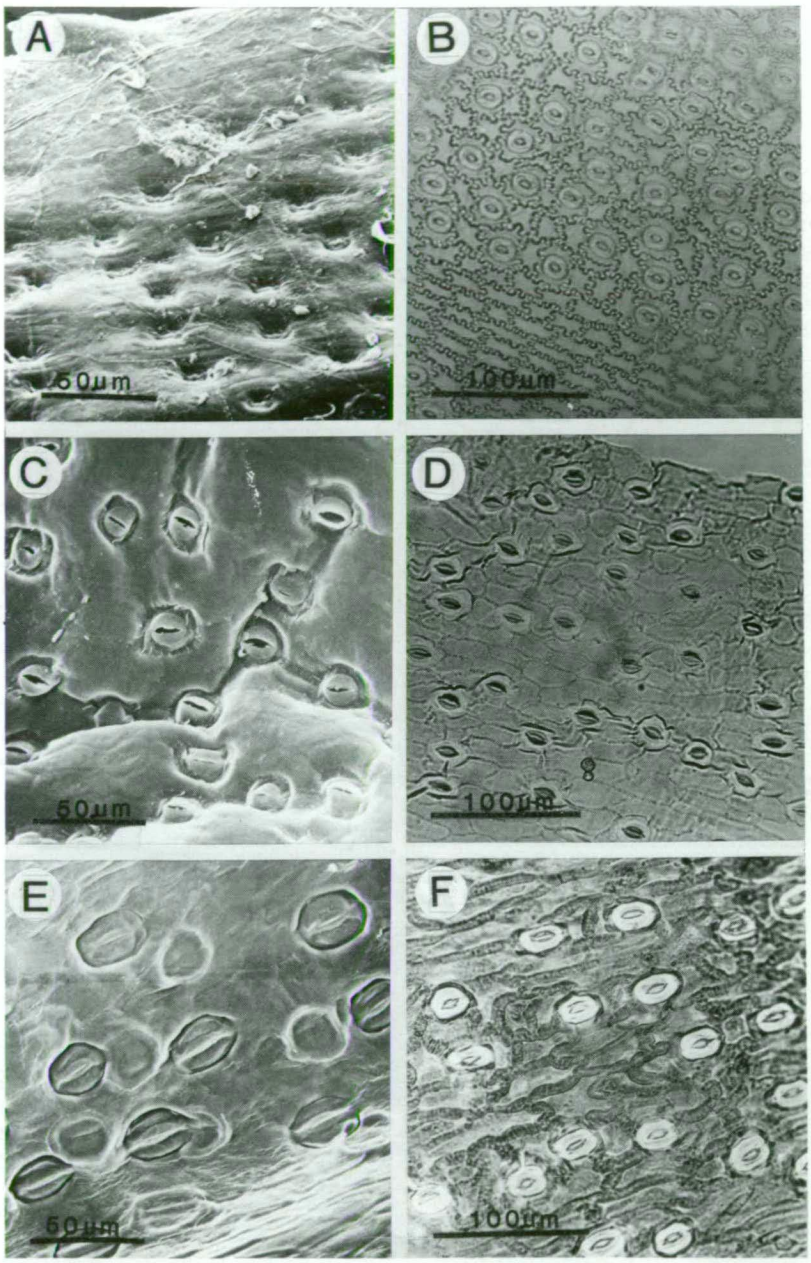

PLATE 3 — A, scanning electron micrograph of extant Dracophyllum minimum *showing small deep stomatal pits; B, cuticular photomicrograph of extant* Dracophyllum minimum *showing small stomata and highly distinctive sinuous epidermal cell walls; C, scanning electron micrograph of extant* Phyllachne colensoi *showing thin cuticle with some local collapse; D, cuticular photomicrograph of extant* Phyllachne colensoi *showing very thin nature of epidermal cell walls; E, scanning electron micrograph of one of the bands of stomata of extant* Abrotanella forsteroides *showing impressions of stomata from closely appressed leaves; F, cuticular photomicrograph of extant* Abrotanella forsteroides *showing distinctive stomatal band and highly thickened epidermal cell walls.*

TABLE 2

Nomenclature and probable correlation of glacial events in the West Coast Range.

	King Drainage System (Kiernan 1980, 1983a)	Henty Drainage System (Colhoun 1985b)	Pieman Drainage System (Sansom 1978, Augustinus 1982)
Last Late Glacial Stage	Dante Glaciation	Margaret Glaciation	Margaret Glaciation
Last Interglacial Stage			
Pre Last Interglacial Glacial Stage(s)	Comstock Glaciations	Henty Glaciation	Boco I & Boco II Glaciations
Late Pliocene/ Early Pleistocene Glacial Stage(s)	Linda Glaciations	Linda Glaciation	Bulgobac I & Bulgobac II Glaciations

tative. Secondly, *all* pollen assemblages are only a partial record of past floras with some indication of abundance (Macphail & McQueen 1983). Thirdly, either extremely rapid accumulation of sediments or in situ growth of a "strong" pollen source may result in the dilution of all or part of the pollen influx, particularly long distance transported types. Neither is considered likely given the high organic content of the silt and abundance of severely under-represented species such as *Donatia novae-zelandiae*, but such considerations are likely to be applicable to any palynofloras recovered from the overlying silts and sands.

The section therefore is interpreted as demonstrating the formation of a tundra soil during a period when the treeline lay below 230 m. *Donatia novae-zelandiae* can occasionally occur to low elevations in areas of reduced plant competition. In New Zealand it occurs at sea level in the far south, and in western Tasmania down to 80 m in the Harwood Valley (M.J. Brown, *pers. comm.* 1983), both in very acid peats. The pollen data strongly suggest a tundra vegetation rather than a valley bog.

Probably the strongest evidence that the reconstruction of the vegetation is correct comes from the close match between the Dante Rivulet assemblage and other near or full glacial period palynofloras recorded in lowland western Tasmania, notably those at Henty Bridge near Queenstown. There Colhoun (1985a) has recorded (subzone HB2, from the top of a unit of lacustrine clays and silts overlying glacial sediments) a Gramineae-Asteraceae-Restionaceae-Cyperaceae assemblage containing significant amounts of Epacridaceae, *Gleichenia* and *Lycopodium*. The major difference is that pollen of Cruciferae occurs in significant amounts whilst Umbelliferae are rare. As at Dante, sclerophyll tree pollen is relatively infrequent at Henty Bridge and rainforest tree pollen such as *Nothofagus cunninghami* virtually absent except in the highest sample (immediately underlying a weathered slope deposit). Colhoun dates this zone as 20–21 kyr b.p., based on a radiocarbon date of 23 640 b.p. from the underlying silts (samples of which contain between 5-10% *N. cunninghami* and 10-40% of *Microstrobos niphophilus* pollen).

Data from Kirkpatrick (1982) indicate that the present climatic treeline in this area of the West Coast lies at 975 m. The fossil *Donatia* and associated pollen evidence suggest minimum depression of the treeline by 750 m assuming this site was at or above the treeline. If the standard lapse rate of 0.6° C/ 100 m is assumed, this suggests that mean annual temperature was depressed by 4.5° C below its present value at this location at approximately 20 000 years B.P.

ACKNOWLEDGEMENTS

We would like to thank Dr J.B. Kirkpatrick for his comments, Dr R.S. Hill for advice on cuticle preparation, Professor E.A. Colhoun for his advice in the field and Mr W. Jablonski for help with the electron microscopy. The radiocarbon dating was funded by the Geography Department, University of Tasmania.

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(accepted 28 November 1986)

Reprinted from

THE JOURNAL OF ECOLOGY
VOL. 74

BLACKWELL SCIENTIFIC PUBLICATIONS
OXFORD LONDON EDINBURGH
BOSTON PALO ALTO MELBOURNE

Journal of Ecology (1986), **74**, 373–384

DISTRIBUTION OF POTENTIAL MACROFOSSILS IN LAKE DOBSON, TASMANIA

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SUMMARY

(1) Lake Dobson is a small lake in south-central Tasmania surrounded by tree- and shrub-dominated sub-alpine evergreen vegetation.

(2) Most species present in the vegetation surrounding Lake Dobson were recovered as leaves from the lake sediment, but the proportions of species changed rapidly between samples, and an accurate reconstruction of the surrounding vegetation from these samples would be impossible except in terms of species present.

(3) *Epacris serpyllifolia*, a small, lakeside shrub, was overwhelmingly dominant in most sediment samples, and was strongly over-represented in relation to its importance in the surrounding vegetation. *Eucalyptus coccifera*, the dominant canopy tree species, was common directly below overhanging trees, but as the leaves sank rapidly they were virtually absent from the rest of the lake. *E. coccifera* was thus strongly under-represented in relation to its importance in the surrounding vegetation.

(4) Leaf remains were far more common in Lake Dobson than reproductive structures and could be more reliably identified.

(5) The most important features affecting leaf deposition in the lake were the prevailing wind direction, the presence of lakeside or overhanging vegetation, and leaf sinking rates. Decomposition of leaves is relatively slow in the lake.

INTRODUCTION

In recent years there has been increased interest in the use of macrofossils in vegetation reconstructions in Australia. However, a poor understanding of the way in which macrofossils reflect the composition of the surrounding vegetation has hampered these reconstructions. Several attempts have been made in Europe and North America to determine the input of potential macrofossils into lake and bog environments, and this work has been summarized by Birks & Birks (1980). The majority of these studies concentrate on fruits and seeds, as they are usually the most important components of macrofossil deposits in those areas. In the southern hemisphere, the two most complete studies have been made in New Zealand (McQueen 1969; Drake & Burrows 1980). These studies concentrated heavily on leaf litter and the results were generally treated qualitatively.

In Australia both Quaternary and Tertiary macrofossil deposits are invariably dominated by leaves. This is probably a reflection of the evergreen nature of the Australian flora, which contains plants with a thick cuticle and a large amount of conductive tissue which resists decomposition. The aim of our research was to study the deposition of leaves in a modern sedimentary environment in Australia to determine how accurately such deposits reflect the surrounding vegetation.

Lake Dobson was selected as the study site for three reasons: (i) it was easily accessible but relatively undisturbed; (ii) the sediments contained large numbers of leaves, reminiscent of the density of leaves in a number of Tertiary deposits in Tasmania; and (iii) the vegetation surrounding the lake contained two of the most important genera in the past and

present Australian flora, *Nothofagus* (Fagaceae) and *Eucalyptus* (Myrtaceae). *Nothofagus* leaves are abundant in Tasmanian Tertiary deposits (Hill 1983a, b, 1984), and *Nothofagus* pollen dominates mid-Tertiary sediments throughout Australia (Martin 1978), whereas *Eucalyptus*, despite its current dominance of the Australian landscape, has rarely been recorded prior to the Quaternary in macrofossil deposits.

MATERIALS AND METHODS

Description of the lake

Lake Dobson is situated in south central Tasmania (42°40'S, 146°50'E) at approximately 1030 m above sea level in the Mt Field National Park. The area has been subjected to a number of glaciations (Kiernan 1983). The lake has been formed by a moraine dam that was probably deposited by a small glacier flowing from Mt Mawson during the last glaciation (Lewis 1922).

Sampling of the lake sediment

Three transects were positioned at 10 m intervals across the centre of Lake Dobson (Fig. 1) parallel to the direction of the prevailing wind. In each transect, samples were collected at 1 m intervals for 10 m away from each shore, at 2 m intervals between 10 and 20 m

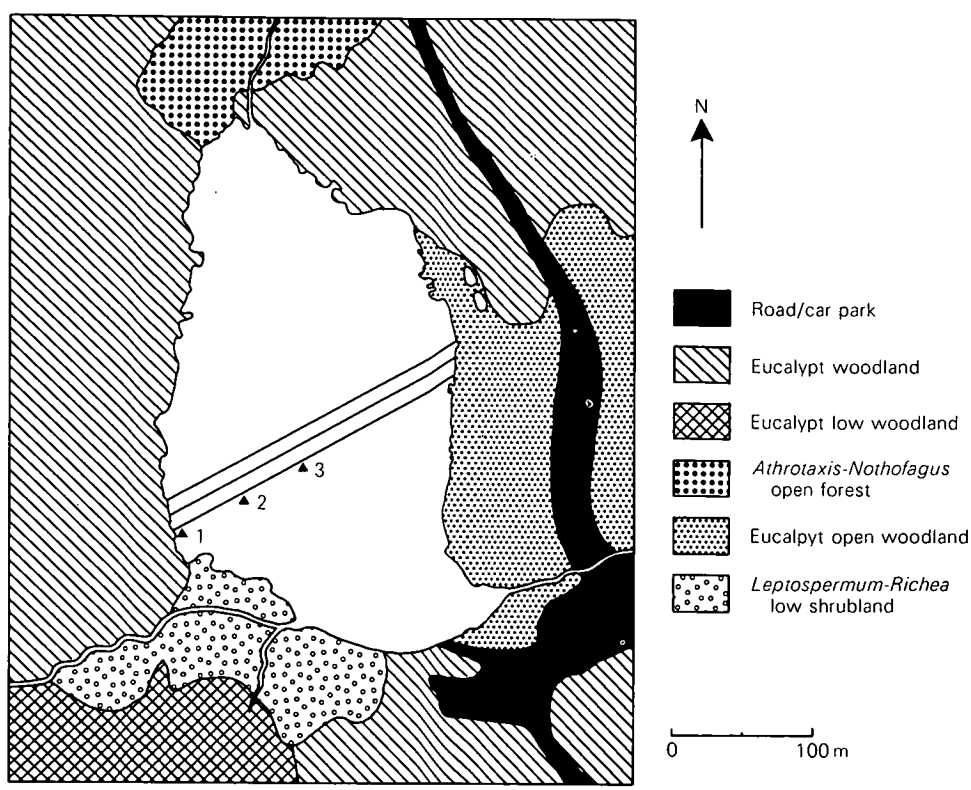


FIG. 1. Map of Lake Dobson showing: the position of the three transects (the three parallel lines; transect 1 is the northernmost; transect 3 the southernmost); the position of the three samples used to measure decomposition of leaves (marked 1, 2 and 3); and the vegetation associations around the lake. The prevailing wind in the area blows from west to east.

from shore, at 5 m intervals between 20 and 40 m from shore, and finally at 10 m intervals in the centre of the lake. Each transect measured 210 m.

Samples were collected in two ways. Close to the shore 500 cm^3 of bottom sediment was collected in a hand-held container, which sampled to a depth of approximately 10 cm. This was necessary due to the abundance of rocks, which made the use of a grab-sampler impossible. Once the sediment took on a uniform small grain size, a 500 cc grab-sampler, which sampled to a depth of approximately 10 cm was employed. Lake depth was recorded along transect 2 at 5 m intervals.

Samples were sieved through a 300 μm sieve. Leaves and all reproductive structures (flowers, fruits and seeds) were retrieved by systematic sorting using a binocular microscope with a magnification of 6·3 times. Due to the large amount of fragmentary leaf material present, only those leaves which were well enough preserved for their length and width to be measurable were retrieved. All specimens were then identified and counted.

Following the counting of leaf samples, 100 mature fresh leaves of the most commonly represented species (*Eucalyptus coccifera*, *Nothofagus cunninghamii*, *Orites revoluta*, *O. acicularis*, *Leptospermum lanigerum*, *Epacris serpyllifolia*, *Trochocarpa cunninghamii* and *Bauera rubioides*) were placed in mesh bags and immersed in the lake at three localities (Fig. 1). These leaves were retrieved after 3 and 6 months and their dry weights compared with controls to determine rates of decomposition. One hundred leaves of the same species, along with 100 1-cm long branches of *Athrotaxis cupressoides* and *Microstrobos niphophilus*, bearing leaves, were floated in water in the laboratory to determine sinking rates. The leaves were agitated for 10 s twice a day, and leaves were removed as they sank. The number of leaves remaining was recorded daily for 100 days.

Species nomenclature follows Curtis (1963, 1967) and Curtis & Morris (1975). Structural terminology follows Specht (1970).

Mapping of the surrounding vegetation

The vegetation surrounding the lake was recorded in three ways: (i) a species list containing all angiosperm and gymnosperm species more than 20 cm tall growing within 50 m of the lake margin was compiled. Voucher specimens of each species were collected to assist in identification of the leaves, fruits and seeds in the lake sediment; (ii) the plant associations occurring around the lake were mapped from aerial photographs and confirmed on the ground; (iii) the position, height, and diameter of canopy of every plant occurring within 10 m of a transect was recorded.

RESULTS

Surrounding vegetation

The vegetation types surrounding Lake Dobson are shown in Fig. 1. With few exceptions the vegetation immediately surrounding the transects had little direct effect on the composition of the samples.

Sample density and diversity

The 156 samples contained many more leaves than reproductive structures (28 788:3970), and many of the reproductive structures were difficult to identify. Therefore the results are restricted to leaves, only 1·4% of which were not identified. Most of the leaves could be identified to a species, but occasionally two closely related species have such a similar leaf morphology that they could not be separated. Table 1 lists all the species

TABLE 1. Angiosperm and gymnosperm species >20 cm tall which occur frequently in the vegetation around Lake Dobson and in the lake sediments. Subjective assessments of species proportions around the western and eastern shores of the lake are given as D (dominant) > C (common) > P (present). An asterisk is used to denote the presence of a species in the lake sediment.

Species	Western	Eastern	Lake
Compositae			
Olearia pinifolia	P	P	*
Cunoniaceae			
Bauera rubioides	C	C	*
Epacridaceae			
Cyathodes glauca	P	P	*
C. juniperina/parvifolia	C	C	*
Epacris serpyllifolia	C	D	*
Richea pandanifolia	C		
R. scoparia/sprengelioides	C	C	*
Trochocarpa cunninghamii	C	C	*
T. thymifolia	P	P	*
Fagaceae			
Nothofagus cunninghamii	C		*
Myrtaceae			
Eucalyptus coccifera	D	C	*
E. subcrenulata	C	C	*
Leptospermum lanigerum	C	C	*
Melaleuca squamea	P	C	
Podocarpaceae			
Microstrobus niphophilus	P	P	*
Proteaceae			
Hakea lissosperma	P	C	
Lomatia polymorpha	P	C	
Orites acicularis	C	C	*
O. diversifolia	P	P	*
O. revoluta	C	C	*
Rubiaceae			
Coprosma nitida	C	C	*
Rutaceae			
Boronia citriodora		C	
Taxodiaceae			
Athrotaxis cupressoides	C	C	*
Winteraceae			
Tasmannia lanceolata	C	C	*

recovered from Lake Dobson, as well as all species recorded within 50 m of the lake margin.

The total number of leaves summed for all transects at each distance from the shore is shown in relation to lake depth in Fig. 2. Similarly, the diversity of the leaf samples at each distance from shore was calculated using Simpson's diversity index (Fig. 2).

The total number of leaves per volume of sediment shows a consistent pattern. There are large numbers close to the shore, which are probably the result of sheltered conditions and input from overhanging trees and shrubs. Beyond the range of overhanging trees (5–10 m) the number of leaves drops substantially and then rises again. This may be a reflection of a change in bottom sediment. Close to the shore there is a large number of small rocks, which were included in the sample. Further from shore the rocky bottom was covered in a deep, fine-grained, organic sediment. The leaves were trapped in this sediment, whereas they tended to settle out through the shoreward rocks. Further away from shore the numbers of leaves decreased substantially.

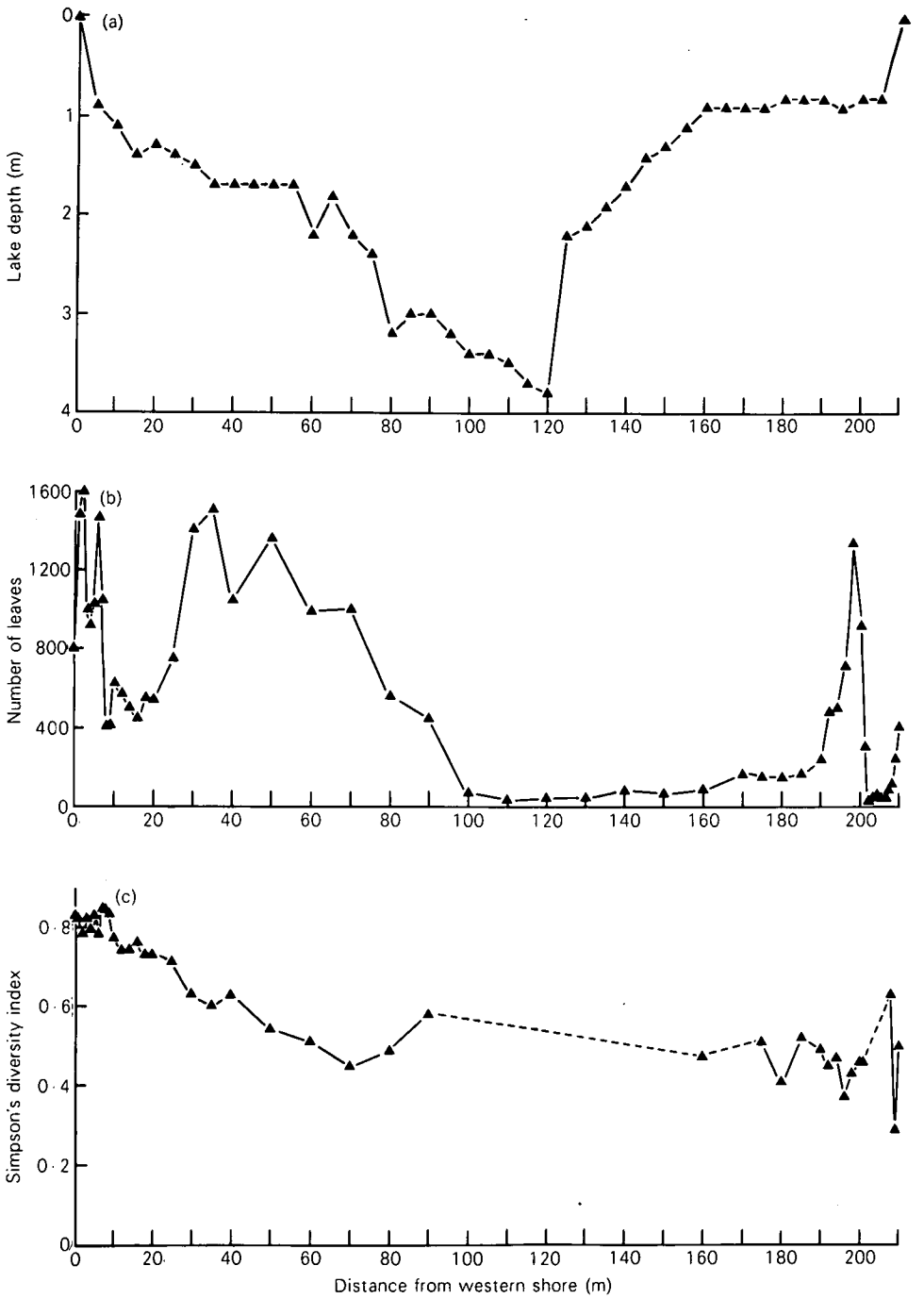


FIG. 2. (a) Lake depth recorded at 5 m intervals along transect 2 on 25 May 1984; (b) total number of leaves at each sampling distance, summed for all three transects; (c) Simpson's diversity index calculated for each sampling distance where the total number of leaves was 25 or more. Broken lines connect non-adjacent points.

This pattern of leaf numbers per volume of sediment was probably a result of the prevailing westerly wind which would be from left to right in Fig. 2. Although the pattern of leaf numbers is the same from both shores, it is extended from the western shore and truncated toward the eastern shore. This suggests that high sinking rates may be a cause of the low numbers of leaves in the central part of the lake.

From the western shore of the lake, the decline in leaf numbers corresponds closely with the increase in depth of the lake. Therefore it is possible that there may be a change in decomposition rates which may be affecting leaf numbers. This possibility is discussed in more detail later.

In general, the diversity of the samples declined from the western to the eastern shore. This decline in diversity was affected most by the increase in dominance of one species, *Epacris serpyllifolia.*

Distribution of species

For species with leaf numbers totalling more than 1% of the whole sample, the percentage at each distance from the shore is plotted in Fig. 3. Two of the gymnosperm species, *Athrotaxis cupressoides* and *Microstrobos niphophilus* occurred in the samples as branch fragments containing several leaves. Since it would have been extremely difficult and time-consuming to count the individual leaves of these species, they were excluded from the calculations of leaf percentages. The number of branch fragments of *A. cupressoides* and *M. niphophilus* were then added to the total leaf numbers, and expressed as a percentage of those totals. The results for each transect are presented separately.

The dominant species in each transect was *Epacris serpyllifolia.* In each transect the percentage of *E. serpyllifolia* was lowest close to the western shore and steadily increased toward the eastern shore. In transects 1 and 2 there was some indication of a decline of *E. serpyllifolia* near the eastern shore. The increasing dominance of this species across the lake probably accounts for the decline in Simpson's diversity index (Fig. 2). *E. serpyllifolia* is a common shrub near the lake edges, and it is probable that it has floated across the lake in the direction of the prevailing wind (west to east). The leaves are small (<2 mm long) and float well (Table 2).

The area close to the western shore was often locally dominated by litter of individual plants which were growing at the lake's edge. This was particularly obvious for *Eucalyptus coccifera* (all transects), *Leptospermum lanigerum* (Transect 2), *Cyathodes juniperina* (Transect 3) and *Epacris serpyllifolia* (Transect 1—a relatively minor peak). The only one of these species which grows about 2 m in height is *E. coccifera.* These trees overhang the lake up to 10 m off-shore, and leaves drop directly into the lake. However, the leaves of this species are very poorly transported, and very few were found beyond the extent of the overhanging trees (e.g. Transect 3). There were few corresponding peaks on the eastern shore, where *Epacris serpyllifolia* was dominant.

Several other species exhibited relatively broad peaks at varying distances from the shore. The most important of these were *Athrotaxis cupressoides, Bauera rubiodes, Orites revoluta, Leptospermum lanigerum, Microstrobos niphophilus,* and *Nothofagus cunninghamii.* The peaks for different species occur at different distances from shore. For example, *Nothofagus cunninghamii* reached a peak in all transects close to the western shore, whereas *Microstrobos niphophilus* had its maximum percentages near the eastern shore Transects 1 and 3) or near both shores (Transect 2). While the position of these peaks reflects the vegetation around the lake to some extent (e.g. there is much more *N. cunninghamii* growing on the western than the eastern shore, and the reverse is true of *M.*

niphophilus), the most important feature of these peaks is that samples taken from different places give a very different interpretation of the surrounding vegetation.

Leaf sinking and decomposition rates

The results of the leaf-floating experiment are shown in Table 2, and the changes in dry weight of leaves submerged in the lake are shown in Table 3. Most species had significant numbers afloat for long periods of time, suggesting that they should be capable of reaching any part of the lake. However, three species were notable exceptions: (i) *Eucalyptus coccifera*—all leaves sank within 2 days. This correlates well with the observation that very few leaves of *E. coccifera* were found beyond the range of overhanging trees in the lake (Fig. 3); (ii) *Orites acicularis*—the majority of leaves sank in 2 days. *O. acicularis* is present in Lake Dobson, but is relatively uncommon. In Transect 1 (Fig. 3) it is clearly congregated near the shore; (iii) *Athrotaxis cupressoides*—all twigs sank within 8 days. Twigs of *A. cupressoides* were congregated close to the shore (Fig. 3), but not any more so than some species which had much lower sinking rates (e.g. *Nothofagus cunninghamii*). In

TABLE 2. Sinking behaviour as the time required for a given percentage of the sample to sink for leaves and stems of the common species encountered in the sediment of Lake Dobson. Individual leaves were used in all cases except for *Athrotaxis cupressoides* and *Microstrobos niphophilus* where 1-cm long twigs bearing leaves were used.

	Time (days)		
Species	25% submerged	50% submerged	75% submerged
Athrotaxis cupressoides	0	0	1
Bauera rubioides	23	28	31
Cyathodes juniperina	12	18	26
Epacris serpyllifolia	19	28	39
Eucalyptus coccifera	0	0	0
Microstrobos niphophilus	4	92	>100
Leptospermum lanigerum	15	19	25
Nothofagus cunninghamii	11	15	36
Orites acicularis	0	0	1
O. revoluta	13	25	37
Trochocarpa cunninghamii	50	67	77

TABLE 3. Average dry weight of leaves of species submerged for 3 and 6 months in Lake Dobson at the three sites marked on Fig. 1. The dry weights are given as percentages of controls (leaves not submerged in the lake).

	Site and time (months)					
	Site 1		Site 2		Site 3	
Species	3	6	3	6	3	6
Bauera rubioides	75	58	67	42	53	42
Cyathodes juniperina	75	65	75	80	55	80
Epacris serpyllifolia	43	58	88	75	48	72
Eucalyptus coccifera	68	64	82	69	69	59
Nothofagus cunninghamii	92	73	81	94	70	78
Leptospermum lanigerum	72	72	83	76	72	62
Orites acicularis	45	58	65	63	62	75
O. revoluta	100	89	78	67	84	67
Mean	71	67	77	71	64	67
Standard deviation	20	11	8	15	12	12

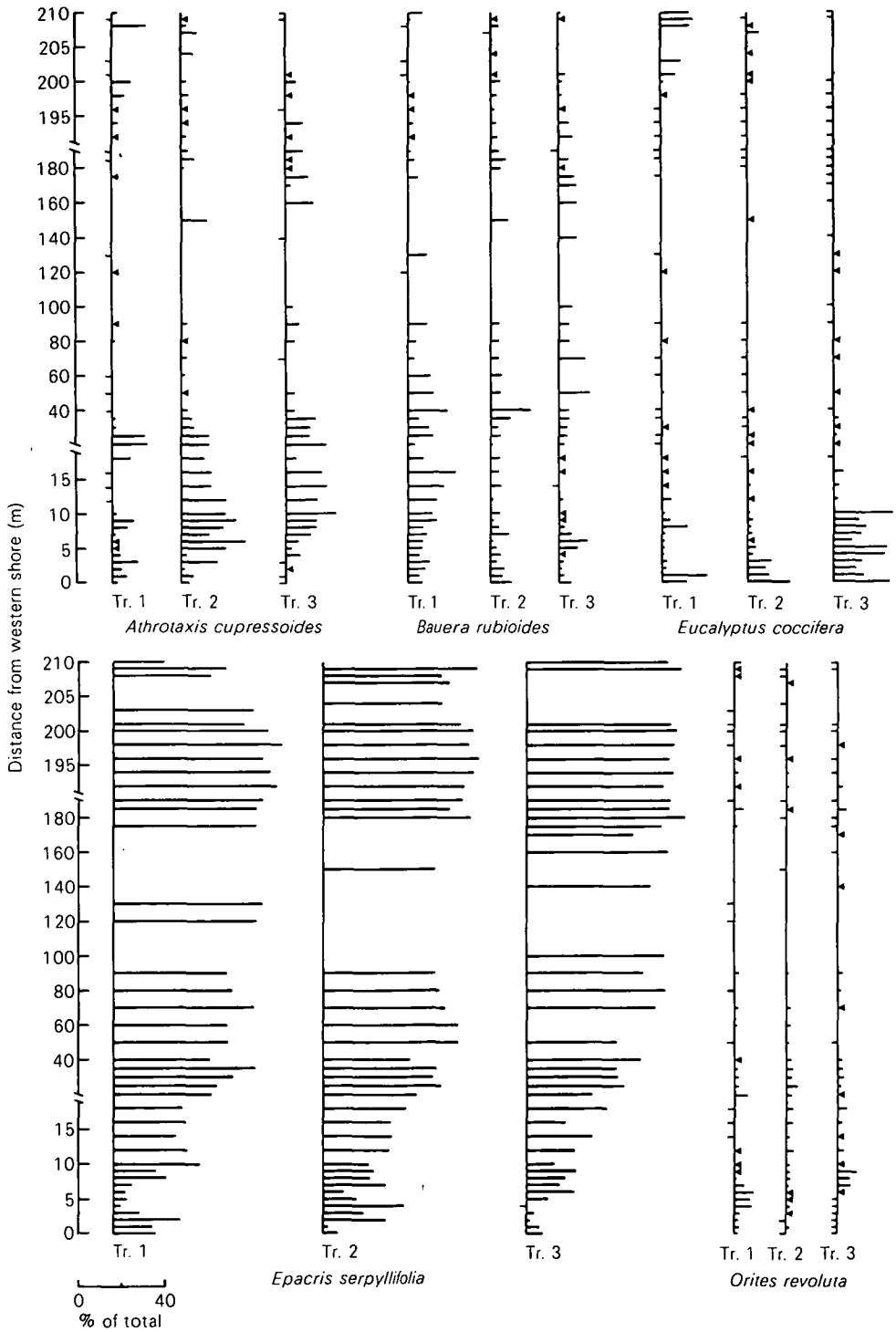
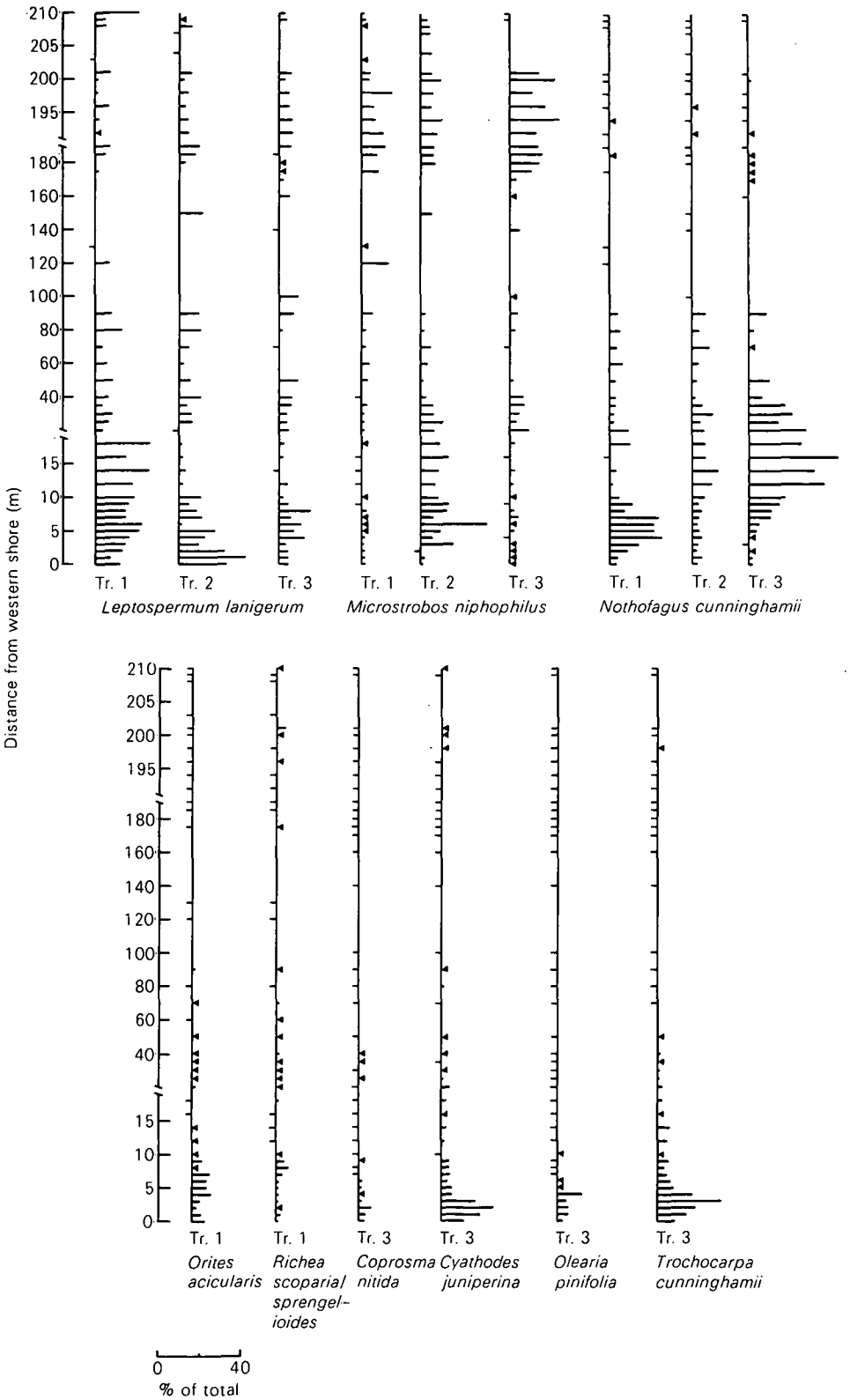


FIG. 3. Percentage occurrence at each sampling point of species contributing more than 1% of and total number of leaves in each transect across Lake Dobson. Arrows indicate a trace occurrence (<1%) or an occurrence in a sample containing <25 leaves. Lines to the left of the axis indicate absence of the species at that point. Samples containing <10 leaves were not considered.


Distance from western shore (m)
210
205
200
195
180
160
140
120
100
80
60
40
15
10
5
0
Tr. 1
Tr. 2
Tr. 3
Leptospermum lanigerum
Microstrobos niphophilus
Nothofagus cunninghamii
Orites acicularis
Richea scoparia/ sprengel-ioides
Coprosma nitida
Cyathodes juniperina
Olearia pinifolia
Trochocarpa cunninghamii
0
40
% of total

general it appeared that all common species with the exception of *Eucalyptus coccifera*, could float for long enough to reach any part of the lake.

All species showed some evidence of decomposition after 3 months submergence in the lake (Table 3). However, despite the decrease in biomass all leaves were still intact and showed no signs of fragmenting. After 6 months there was little increase in decomposition (Table 3), suggesting that, after an initial rapid decomposition, there is very slow decay of more resistant tissues. All leaves were still intact after 6 months. There appears to be little difference in decomposition rates between the three sites, although there are some clear inconsistencies which suggest that further work needs to be done before such conclusions can be drawn.

It is therefore likely that some of the leaves collected and scored from Lake Dobson may have been in the lake for several years, since many were more decomposed than those recovered after 6 months submergence. Although they are not directly comparable, these results for decomposition are very different from those obtained by Spicer (1981), who reported considerable lamina loss in some deciduous species submerged in Silwood Lake, England, for 2–4 months.

Long-distance transport

All but a few of the leaves recovered clearly had their source in the lakeside vegetation. However, five species were recorded which have not been observed within 50 m of Lake Dobson (Table 1). Two of these species, *Nothofagus gunnii* and *Phyllocladus asplenifolius*, have not been observed within 1 km of the lake. *N. gunnii* is Australia's only winter-deciduous species, and occurs on the slopes both above and below Lake Dobson. It was represented by a single leaf, which was probably the result of a chance long-distance dispersal event, probably via the strong winds which are common in the area. *P. asplenifolius* was represented by several phylloclades, but they occurred in a very restricted area close to the shore. This species is preferentially grazed by macropods, and it is possible that a small branch has been transported to the lake by an animal. None of the five species was present in more than trace amounts.

DISCUSSION

The species composition of the sediment samples from Lake Dobson was a relatively accurate reflection of the surrounding vegetation in terms of species present (Table 1). Twenty-two of the thirty-four shrub and tree species recorded from the lake perimeter were recovered from the samples, and most of those which were not found were uncommon close to the lake margin. There was also very little long-distance input, with only trace amounts of five non-local species being recorded. No herb species were recorded from the lake sediment.

In terms of representation of species, the most important features were that one species, *Epacris serpyllifolia*, was vastly over-represented, while the dominant canopy species, *Eucalyptus coccifera* was greatly under-represented. *Epacris serpyllifolia* is a small shrub around the lake margins, forming only a minor component of the lakeside vegetation. The extreme dominance of this species in the sediment is difficult to explain. The leaves appear to sink and decay at rates comparable with those of other species (Tables 2 and 3), and it does not appear to produce excessive amounts of litter, although no quantitative data are available. One feature of this species which could be important is that it has very small leaves, and since only complete leaves were considered in this study, it may be expected

that small leaves would remain intact for longer than relatively large leaves. Therefore the *E. serpyllifolia* leaves sampled may cover a greater time span than other species. However, in the centre of the lake *E. serpyllifolia* was often the only recognizable leaf material present, including fragments, suggesting that fragmentation is not the only important feature.

Eucalyptus coccifera is the major canopy species around the lake, interspersed with occasional *E. subcrenulata* trees. The major reason for the under-representation of this species was its inability to float. Very few leaves or leaf fragments of *E. coccifera* were observed beyond the trees overhanging the lake. In the fine sediment, more than about 15 m offshore, where fossilization would be most likely to take place, *E. coccifera* was virtually absent. This is interesting, since *Eucalyptus* species are now the dominant canopy species in most non-rainforest vegetation in Australia, and yet the macrofossil evidence of the genus is very poor (Lange 1978; Holmes, Holmes & Martin 1983). While there is strong evidence that *Eucalyptus* has only relatively recently assumed this dominance on a broad scale (Singh, Kershaw & Clark 1981), it is possible that the poor dispersal of leaves may also be an important factor affecting its low representation in the macrofossil record.

Most other species appeared to be present in the samples more or less in proportion to their presence in the surrounding vegetation. The very strong effect of the prevailing wind in distributing large amounts of litter away from the western shore meant that species occurring there were particularly well represented in the sediment—e.g. *Athrotaxis cupressoides*, *Bauera rubioides*, *Orites revoluta*, *Epacris serpyllifolia*, *Leptospermum lanigerum* and *Nothofagus cunninghamii* (Fig. 3). If the shore effect is ignored (i.e. if only those samples more than about 15 m offshore are considered) then the samples would predict a vegetation with a canopy of *Athrotaxis cupressoides* and *Nothofagus cunninghamii*, with a diverse understorey dominated by *Epacris serpyllifolia*. This is in contrast to the actual vegetation, which is dominated by *Eucalyptus coccifera* in the canopy, with a diverse understorey which is lacking in dominants.

The dominance of leaves rather than reproductive structures makes an interesting comparison with Australian fossil deposits. Although reproductive structures are sometimes recovered from Tertiary macrofloras (Christophel 1980, 1984; Christophel & Basinger 1982; Hill 1983a), leaves are overwhelmingly dominant (Hill 1982). This is in direct contrast to the northern hemisphere, where reproductive structures are relatively common (Birks & Birks 1980; GreatRex 1983) and is probably a reflection of the different decomposition rates of evergreen and deciduous leaves. Because of this, leaves will always be the most important angiosperm macrofossils in the southern hemisphere, and therefore it is important to learn more about their representation in modern sedimentary environments.

ACKNOWLEDGMENTS

We thank the Tasmanian National Parks and Wildife Service for permission to work in the Mt Field National Park and Natalie Brown for field assistance. This research was supported by the Australian Research Grants Scheme.

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(Received 27 March 1985)

Papers and Proceedings of the Royal Society of Tasmania, Volume 118, 1984

(ms. received 7.XI.1983)

IMPACT OF TRAMPLING ON BOLSTER HEATH COMMUNITIES OF MT FIELD NATIONAL PARK, TASMANIA

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(with four tables, one text-figure and three plates)

ABSTRACT

GIBSON, N., 1984 (31 viii): Impact of trampling on bolster heath communities of Mt Field National Park, Tasmania. *Pap. Proc. R. Soc. Tasm.*, 118: 47-52, pls 1-3. ISSN 0080-4703. Department of Geography, University of Tasmania, Hobart, Tasmania, Australia.

The impact of trampling on the alpine bolster heath communities of Newdegate Pass and the Mt Field West plateau (1300-1400 m) were investigated. It was found that in the track vegetation, percentage bare ground was significantly higher, and percentage cover of some taxa and species diversity were significantly lower than in the surrounding undisturbed vegetation. Degradation was measurably worse on sections of the track subject to water-logging. Implications of these findings for recreational management are discussed.

INTRODUCTION

As leisure time increases and society becomes more urbanized the usage of national parks will increase. Natural vegetation varies in its ability to sustain use without degradation (Liddle 1975a, b). Alpine vegetation is particularly susceptible to damage caused by walking along tracks due to its slow growth rate and short growing season (Willard & Marr 1970a, Billings 1973, Liddle 1975b).

Calais (1981) studied the impact of walking tracks on the vegetation of the Cradle Mountain-Lake St Clair National Park. He found significant damage occurred to alpine heath communities with as few as 500 passages/year. This threshold was defined as that amount of trampling which reduces the vegetation cover sufficiently to expose soil to erosion without precluding recovery. Further use above this level results in erosion of the soil layer to pavement, from which recovery is exceedingly slow.

The present study looks at the impact of trampling on the bolster heath communities at Newdegate Pass (1300 m) and the Mt Field West plateau (1400 m) (42°41'S, 146°30'E). Visitor usage data are not available but vegetation damage from trampling is apparent.

The bolster heath of both sites occurs intermixed with areas of coniferous heath and lichen covered dolerite boulders. The major bolster species are *Abrotanella forsteroides*, *Donatia novae-zelandiae*, *Dracophyllum minimum* and *Pterygopappus lawrencii* which can occur alone or in complex mosaics. These species are highly branched chaemaephytes with extremely short internodes. They can easily support the weight of a man. Single bolsters may be up to 2.5 m in diameter and almost 1 m tall.

Both areas are flat or gently sloping, with an acid peat soil of about 0.5 m developed over Jurassic dolerite country rock. No direct climatic data are available but records from the nearest meterological station indicate an annual rainfall of about 1500 mm with a winter maximum, and mean annual maximum temperature of about 10°C and mean annual minimum temperature of about 0°C. Snowfalls can occur at any time of the year, and the soil profile can freeze to depths of 0.5 m in winter.

Species nomenclature follows Curtis (1963, 1967), Curtis & Morris (1975) and Costin *et al.* (1979) except where otherwise indicated. Structural terminology follows Kirkpatrick (1983). The term bolster rather than cushion plant has been used to denote the hard compact nature of these species compared with the much softer northern hemisphere cushion species.

Impact of Trampling on Bolster Heath Communities

METHODS

To assess trampling damage three paired transects were established at Newdegate Pass (NP1-NP3) and two paired transects on the Field West plateau (FW1-FW2). The paired transects consisted of a set of 20 contiguous 25 cm square quadrats laid down the centre line of the track with another set parallel to this but 2 m into apparently undisturbed vegetation. A further transect was run at right angles to the track and a levelled profile constructed.

With each quadrat species occurrence was recorded and percentage overlapping cover was estimated using 25 equal subdivisions. Where a cover value of less than 5% was recorded in the field a value of 2% was assumed for the purpose of analysis.

The data were analysed using the nonparametric 2-tailed Mann-Whitney U test to test for significant differences between percentage cover of species in the track and undisturbed vegetation for the combined data set from five paired transects (Siegel 1956).

The diversity index $N_2 = [(\Sigma x)^2]/\Sigma x^2$ of Hill (1973) was calculated for each paired transect, where x = percentage cover of each species which occurs. A similarity index was also calculated: C = a/c, where a = number of shared species, and c = total number of species.

RESULTS AND DISCUSSION

The communities at each transect are described in table 1. Species for which significant differences ($P < 0.01$) in mean cover values were found from the combined data set are shown in table 2. Differences in mean percentage bare ground are detailed in table 3. Species number in each transect pair, and diversity and similarity indexes, are shown in table 4.

The effect of walking on these bolsters is to wear a distinct track generally about 25 cm wide (plates 1 & 2, fig. 1). In all cases percentage bare ground is significantly higher in the track vegetation although the magnitude of this difference varies (table 3). Areas subject to continuous seepage such as NP3 and FW1 have the highest percentages of bare ground in the trampled areas. Indeed percentage bare ground appears to give an excellent index of the saturation of the bolster peats at any point of the track on areas of low slope (cf. Willard & Marr 1970a).

TABLE 1

TRANSECT VEGETATION
Description of plant communities and soil moisture.

Newdegate Pass Transect 1 (NP1):	*Microcachrys-Donatia-Oreobolus pumilio-Dracophyllum* bolster heath on a gentle slope rarely subject to waterlogging.
Newdegate Pass Transect 2 (NP2):	*Donatia-Dracophyllum-Pterygopappus-Empodisma* bolster heath on a gentle slope rarely subject to waterlogging.
Newdegate Pass Transect 3 (NP3):	*Empodisma-Dracophyllum-Donatia* bolster heath on flat subject to continuous seepage.
Field West Transect 1 (FW1):	*Donatia-Dracophyllum-Empodisma-Celmisia saxifraga* bolster heath on flat subject to periodical waterlogging.
Field West Transect 2 (FW2):	*Dracophyllum* bolster heath on slight slope, rarely subject to waterlogging.

Plate 1 - Track through *Microcachrys* bolster heath at Newdegate Pass Transect 1.

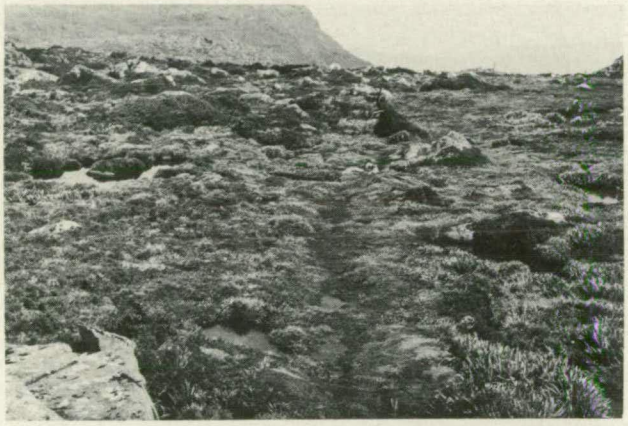

Plate 2 - Damage of track through waterlogged bolster heath at Newdegate Pass.

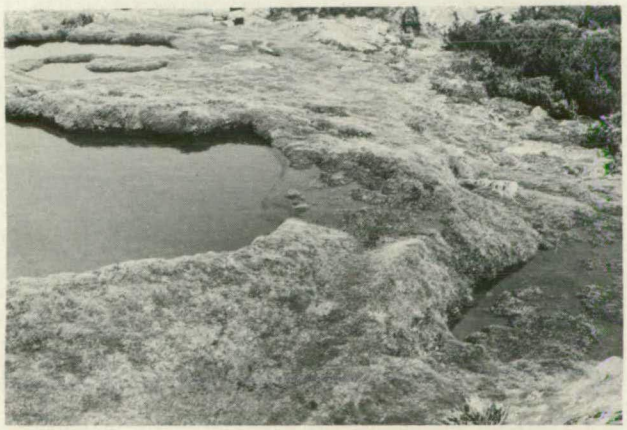

Plate 3 - Damage to bolster wall of tarn at Newdegate Pass resulting from track.

TABLE 2

PLANT TAXA
Combined list of taxa showing those for which a significant difference between track and undisturbed vegetation exists.

*Empodisma minus****	*Donatia novae-zelandiae*
*Celmisia saxifraga****	*Dracophyllum minimum*
Lichen spp.***	*Michrocachrys tetragona*
*Pterygopappus lawrencii****	*Drosera arcturi*
*Erigeron stellatus****	*Carpha alpina*
*Epacris serpyllifolia****	*Garmedia fitzgeraldii* F. Muell. & Rodway
*Cyathodes dealbata****	*Sprengelia incarnata*
*Gentianella diemensis****	*Mitrasacme archeri*
Rhacomitrium spp.***	*Actinotus suffocata*
*Celmisia longifolia****	*Pentachondra pumila*
Moss spp.**	*Oreobolus acutifolius*
*Danthonia pauciflora***	*Astelia alpina*
Carpha spp.**	*Drimys lanceolata*
*Oreobolus pumilio**	Unidentified grass spp.
*Dislaspis cordifolia**	

* $P \leq 0.01$ ** $P \leq 0.001$ *** $P \leq 0.0001$

Except for NP3 and FW1 transects, bare ground resulted from the death of bolster species on the track and not from disruption of the soil profile. In NP3 and to a lesser extent FW1 the soil profile has become churned by boot traffic especially at times of saturation of the soil profile.

No species had a higher mean cover in the track vegetation. Those significantly lower are listed in table 2. The taxa that were most noticeably reduced were *Empodisma minus*, *Celmisia saxifraga*, lichen spp., *Microcachrys tetragona* (highly significant in NP1 but not reflected in the combined data). Other species which were also highly susceptible are *Pterygopappus lawrencii*, *Erigeron stellatus*, *Epacris serpyllifolia*, *Cyathodes dealbata*, *Gentianella diemensis*, *Rhacomitrium* spp. and *Celmisia longifolia*. Some of these species had low cover values. The harder bolster species *Donatia novae-zelandiae* and *Dracophyllum minimum* are generally more resistant. These results are in strong agreement with those of Calais (1981) and generally support the assertion of Liddle (1975) that plants with basal apices and meristems tolerate trampling better than those which do not have such structure.

The lesser number of species on the tracks is generally a reduction rather than substitution of different species in the track vegetation (table 4). This is further indicated by the high values of the similarity index (table 4). The lower value for NP3 reflects the drastic reduction in number of species in the track vegetation. Similar reduction of species on tracks has been documented elsewhere (Hoffman & Alliende 1982).

TABLE 3

PERCENTAGE BARE GROUND

	NP1		NP2		NP3		FW1		FW2	
	$\bar{x}$	sd	$\bar{x}$	sd	$\bar{x}$	sd	$\bar{x}$	sd	$\bar{x}$	sd
Undisturbed vegetation	0.60	1.96	0.00	0.00	0.80	1.69	0.00	0.00	3.72	3.40
Track vegetation	8.92	8.64	23.40	16.52	82.40	12.88	45.40	16.24	26.00	19.00

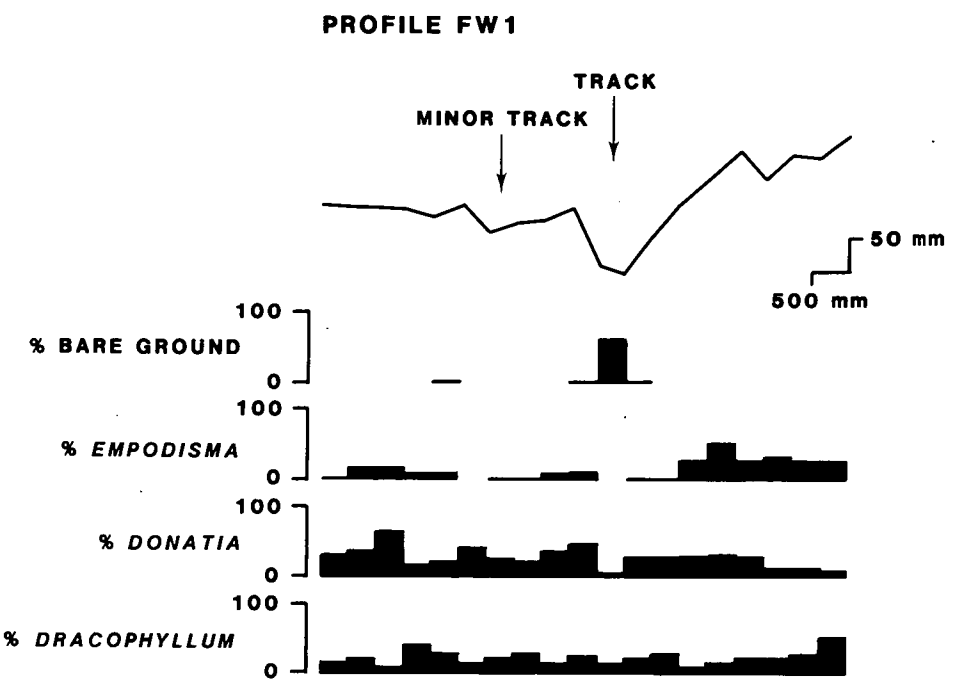

FIG. 1 - Profile transect of Field West transect 1 (FW1) showing percentage bare ground and percentage cover of dominant taxa, *Empodisma minus*, *Donatia novae-zelandiae* and *Dracophyllum minimum*.

The diversity index (table 4) shows a wide spread for these bolster heath communities reflecting their large degree of heterogeneity. In every transect however the diversity index of the track vegetation was lower than that of the undisturbed vegetation. Others have reported a variable response of diversity to trampling, depending on such factors as intensity of wear and condition of untrampled controls (Liddle 1975a).

CONCLUSIONS

This study has shown that damage to bolster heath communities, resulting from walking tracks, is variable. Sites with high soil moisture show the greatest damage. Indeed these sites, even with present relatively low usage, are at a critical stage because the soil profile, generally of a somewhat structured peat, is breaking down and eroding (Liddle 1975a, Willard & Marr 1970a, Calais 1981). It has been reported by others that once soil disturbance has occurred re-establishment is very difficult and slow (Billings 1973), perhaps of the order of hundreds of years (Willard & Marr 1970b).

On the low slope areas of Newdegate Pass and the Mt Field West plateau trampling on most sections of the track has not destroyed more than 50% of vegetative cover nor broken down the soil profile. Thus present usage is at or below the carrying capacity of this area, where carrying capacity is defined as the annual net primary production being equal to or greater than the annual amount of plant material destroyed by trampling. This is not the case on the wetter sections of the track where moderate levels of damage are apparent and tracks are beginning to spread laterally.

TABLE 4

NUMBER OF SPECIES, DIVERSITY INDEX (N_2) AND SIMILARITY INDEX (C). Definitions of N_2 and C are given in the text.

		NP1	NP2	NP3	FW1	FW2
Number of species	Undisturbed vegetation	21	21	23	16	12
	Track vegetation	17	17	8	16	8
N_2	Undisturbed vegetation	5.76	6.31	7.26	7.41	1.42
	Track vegetation	4.96	3.71	3.70	4.01	1.13
C		0.73	0.81	0.35	0.78	0.75

The data argue for the re-routing of tracks around persistent wet areas or installation of raised boardwalks. These measures would also protect associated geomorphological/biogeomorphological features, notably the small and fragile tarns dammed back by the bolster plants (plate 3).

ACKNOWLEDGEMENTS

I would like to thank the National Parks and Wildlife Service for permission to work in the park, Dr J.B. Kirkpatrick for comments on an earlier draft, Dr G. van de Geer for drafting the figure and Terese Hughes for typing the manuscript.

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